Long-term patterns of mortality and regeneration in near-natural woodland

Thesis

Long-term patterns of mortality and regeneration in near-natural woodland

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Discipline: Woodland Ecology

A thesis submitted in partial fulfilment of the requirements of the Open University for the degree of Doctor of Philosophy.

Harper Adams University College

September 2004

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ABSTRACT

1. Long-term patterns of natural regeneration, growth, mortality and disturbance were recorded in six native lowland woods around Britain, using a series of permanent transects/plots established during the 1950-80s. Records were made including the position and status of trees, shrubs, established seedlings, dead wood and canopy gaps.
2. The stands inherited various original-natural features and grew away from a managed state. Nonetheless, their structure and composition remained heavily influenced by past treatment and non-native species.
3. The natural development of five woodland types and twelve tree and shrub species was reviewed and four general stages of stand development were recognised.
4. The major processes controlling stand development were: (i) exclusion; (ii) damage caused by wind, drought, large herbivores and grey squirrels; and (iii) regeneration and release below part-broken stands and within/around larger canopy gaps.
5. The main structural changes identified during stand development were: (i) an increase in basal area to a maximum of c.30-50m^2 ha^{-1}; (ii) a decline in stem density until understorey reinitiation/gap-phase regeneration occurred; (iii) an increase in stratification, especially under lighter crowned trees and once reinitiation/regeneration occurred; (iv) a scarcity of canopy gaps until at least 125-150 years growth, after which gap creation tended to be patchy and mainly associated with windstorms and drought, though an extensive blow down was recorded; and (v) a scarcity of dead wood until stands matured and broke-up.
6. Compared to other temperate forests, several distinctive aspects of stand development were recognised, particularly: (i) the role of large herbivores in delaying and altering regeneration; (ii) the importance of debarking by grey squirrels; (iii) the potential for some canopy gaps to fill other than with tree regeneration; (iv) the persistence of the understorey in certain native stand types; and (v) the vulnerability of mature beech stands to sudden and quite extensive collapse.

ACKNOWLEDGEMENTS

I am grateful to Dr. Andy Wilcox, Dr. George Peterken and Dr. Ian Trueman for their supervisory support and guidance. All commented on the thesis structure and content and gave valuable suggestions for improvement. In addition, Andy Wilcox worked hard to maintain my motivation, George Peterken introduced me to the subject, identified the study sites, and encouraged my interest throughout, and Ian Trueman patiently discussed how the field data could be focused.

I also gratefully acknowledge the support of the European Union under the RENFORS (Regeneration of Native Forest Stands for timber production and environmental value) and Nat-Man (Nature-Based Management of Beech in Europe) projects, which were conducted in the UK by Ecoscope Applied Ecologists and the Oxford Forestry Institute (Oxford University).

I would like to thank English Nature/Scottish Natural Heritage (and their predecessors), Sussex Wildlife Trust, The Forestry Commission, The National Trust, and Nigel Anderson, who kindly allowed access to the study sites and have protected and maintained them as minimum-intervention reserves.

Several people facilitated access and kindly provided useful information on the study sites, including: George Peterken (all sites), David Burton (Langley), Simon Furmage (Clairinsh), Dave Hutton (Toy's Hill), and Tony Whitbread (The Mens).

All the studies extended in this thesis were initiated and sustained through the work of earlier organisers and recorders. Particularly important have been: George Peterken (all sites); Christa Backmeroff (Clairinsh, Langley, Monks); Ken Wallace (Clairinsh); Noel Chadwick, Peter Edwards, Joyce Lambert, John Manners, Tiffany Passmore, Joanna

Prastka, Ankie Visschedijk (Denny); Simon Davey, Frank Docherty and Tony Whitbread (The Mens); and Dave Hutton (Toy's Hill).

In addition, many people kindly helped with the fieldwork, including: Duncan Brown, Simon Furmage, John Gibson, Collin Horne, Donna MacLean, Andy MacGregor, Bridget Primrose, Dorothy Simpson (Clairinsh); Michael Fenner, George Peterken (Denny); David Burton, Nigel Cowling, Albert Knott, John Lobb, Linda Smith (Langley); Don Davies, Iain Webb (Monks); Jill Barton, Frank Docherty, Emma Marchant, David Randall (The Mens); and Dave Hutton, David Paine, Alisa Savage (Toy's Hill).

I have been fortunate to have the following researchers take me to a number of natural woodland reserves in continental Europe: Richard Bradshaw, Jurij Diaci, Jens Emborg, Katrine Hahn, Ad van Hees, Dušan Roženbergar, Tibor Standovár and Tomáš Vrška.

Finally, I am particularly grateful to my wife, Anne, who helped with much of the fieldwork at Denny, Langley Wood and Monks Wood, put up with many late-night stretches, and encouraged me to finish what had been started.

LIST OF PUBLISHED MATERIAL

The following papers and reports based on this thesis have been published.

(i) Mountford, E.P., Peterken, G.F., Edwards, P.J. & Manners, J.G. (1999) Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Ecology, Evolution and Systematics 2, 223-272.

(ii) Mountford, E.P. (2000) Long-term stand change in a near-natural oakwood on Clairinsh Island, Scotland. In: Kirby, K.J. and Morecroft, M.D. (eds.) Long-term studies in British Woodland. English Nature Science Series Number 34. English Nature, Peterborough. 19-31.

(iii) Mountford, E.P. & Peterken, G.F. (1998) Monitoring natural stand change in Monks Wood National Nature Reserve. English Nature Research Report Number 270. English Nature, Peterborough.

(iv) Mountford, E.P., Peterken, G.F. & Burton, D. (1998) Long-term monitoring and management of Langley Wood: a minimum-intervention National Nature Reserve. English Nature Research Report Number 302. English Nature, Peterborough.

(v) Mountford, E.P. & Peterken, G.F. (2000) Natural developments at Scords Wood, Toy's Hill, Kent, since the Great Storm of October 1987. English Nature Research Report Number 346. English Nature, Peterborough.

(vi) Mountford, E.P. and Peterken, G.F. (2001) Long-term changes in an area of The Mens, a minimum-intervention woodland damaged by the Great Storm of 1987. English Nature Research Report Number 435. English Nature, Peterborough.

(vii) Mountford, E.P. (2002) Monitoring of beechwoods in southern England damaged by the Great Storm of 1987. In: Brunner, A. (ed.) Restocking of storm-felled forests: new approaches. Danish Centre for Forest, Landscape and Planning Reports Number 12, 83-86.

1. INTRODUCTION

1.1. General aims

Since the late 19th century and particularly during the last 40 years of the 20th century, our understanding of how natural woodland develops in the North Temperate Zone, and the forms it adopts, has been greatly increased. Understandably, most of this work has been based on studies in North America and montane continental Europe where natural woodland has survived in some quantity. Amongst the many insights, it has been learnt that disturbances of various kinds play a major role in the dynamics of natural woodland and thereby constitute a major determinant of woodland structure and composition. In addition, natural woodland varies in its dynamics, structure and composition from one part of the North Temperate Zone to another. This increased understanding not only helps in the development of basic ecological theory, but has also proved to be of value in the management of woodland.

The problem for ecologists in Britain (and other parts of north-west Europe) is that only a few near-natural woods remain from which the natural state of local woodland can be understood. Given the scarcity of natural reference points, conjecture must be based on inferences from the impact of natural events and periods of neglect in semi-natural woods, and from extrapolation of natural woodland elsewhere and sub-fossil records of past woodland (extrapolation through time). Whilst this supplies some insights, it still leaves a good deal of uncertainty. Accordingly, in Britain (as elsewhere) a number of minimum-intervention research reserves have been established which will eventually allow the dynamics, structure and composition of local natural woodland to be better understood. This study forms part of the development of this research. It builds on a set of permanent plot records made in six minimum-intervention reserves in lowland Britain. It aimed to use information from this and other relevant research to:

'make a synthesis on the potential natural development of a range of native trees/shrubs and deciduous woodland types in lowland Britain, identifying the main stages of stand development and the major processes and main structural characteristics associated with these'.

The object, broadly speaking, was to increase our understanding of the characteristics, potential states and processes that operate in near-natural woodland reserves in modern-day lowland Britain, through the direct observation of actual changes that have taken place in a representative set of sites. The material presented also serves as a contribution to vegetation science, as a guide for scientific studies based on permanent plots, and as a reference for the application of minimum-intervention management and nature-based forestry.

It should be noted that long-term studies of this sort are essentially open-ended. Unlike experimental scientific studies, they do not start with a strict hypothesis that is then put to the test, at which point the study concludes. Rather, they start with a broad objective and a judgement as to what features will be useful to record, acknowledging that one cannot know precisely what events will take place, nor what processes will operate. For these and other reasons, such studies are closer to historical investigations than classical scientific research: they tend to make the best use of what happens to be available.

1.2. Natural stand development in temperate woodland

1.2.1. Defining a stand

A stand can be defined as a group of trees and shrubs growing under similar conditions with a similar composition and recent history. Stands in natural temperate woodland usually comprise a mixture of deciduous trees and shrubs, sometimes with an admix of conifers (see Jahn 1991, Röhrig & Ulrich 1991), and with individual trees potentially

growing for many centuries and to 25-40m or more in height. Nevertheless, a stand is a rather broadly defined concept. There is no precise limit to the size and shape of a stand: it can refer to patches of woodland ranging in scale from a few trees to several hundreds of hectares with general similarities. Nor is their any certainty that a stand will develop coherently, especially given that windstorms and other natural disturbances tend to have a patchy impact across the landscape and within individual stands. Thus, scale issues are integral to any discussion of stand dynamics.

1.2.2. Outline of natural stand development

Natural stand development is concerned with how and why woodland stands and their associated features change over time. Many aspects of this subject are covered in the textbook of Oliver & Larson (1996), which is based mainly on literature from temperate woodland in North America where survival and study of natural woodland remnants/dynamics is relatively common. A second major work is that of Peterken (1996), whose textbook covers the ecology and conservation of natural woodland in northern temperate zones, citing literature from Europe as well as North America. Major works on the natural stand dynamics of east-central European woodland reserves include Leibundgut (1982), Mayer (1984), Průša (1985), Mayer *et al.* (1987) and Korpel' (1995), whilst Faliński (1986) examined many aspects of the ecology of the famous Białowieża Forest in Poland. In addition, the publications of the European Union COST Action E4 'Forest Reserves Research Network' give information on important research sites and related studies (Diaci 1998, Parviainen *et al.* 1999, 2000, Parviainen 2000).

Natural stand development is dictated by the basic demographic factors that control all plant populations, i.e. birth, growth and mortality. Stands are initiated, grow, and eventually break-up and are replaced. This sequence is most rigidly defined in even-aged plantations, where a series of growth stages can be precisely defined. In natural woodland

the cycle is generally less orderly, but nevertheless, several ecologists have defined various stages or phases of development. For simplicity, the outline below adopts the stages defined by Oliver & Larson (1996) and Oldeman (1990), though comparable stages have been devised for natural woodland in east-central Europe (see works listed above).

Stands start out by regenerating during a 'stand initiation stage' (Oliver & Larson 1996) or 'innovation phase' (Oldeman 1990). Trees and shrubs often regenerate in even-aged cohorts where a disturbance has created a gap in the canopy and allowed an influx of light. This is sometimes referred to as 'gap-phase' regeneration (Watt 1947). Smaller gaps are usually filled by shade-tolerant species, which often establish as small saplings or 'advance regeneration' prior to gap creation, whereas light-demanding species are often better able to disperse into the centre of large gaps and grow faster there than shade-tolerant species (e.g. Watt 1923-25, Bormann & Likens 1979, Poulson & Platt 1989). Regeneration is, however, influenced by many other factors, including seed production, predation, germination, disease, competition from ground vegetation, frost-damage, drought and herbivory (e.g. Canham & Marks 1985, Connell 1989, Platt & Strong 1989, Veblen 1992, Oliver & Larson 1996, Peterken 1996).

Once a new stand has initiated it enters a 'stem exclusion stage' (Oliver & Larson 1996) or 'aggradation phase' (Oldeman 1990). This starts once the canopy closes. As the trees and shrubs grow larger they compete for light, water and nutrients. Some survive and eventually grow into mature trees, but many become overtopped, are starved of light and nutrients, and gradually are excluded (Peet & Christensen 1987, Waring 1987). During this stage regeneration ceases and development is generally determined by the stand composition at the outset (i.e. the initial floristic composition) (Egler 1954). Depending on the initial composition, stands may progress from an initial phase where fast-growing, light-demanding, 'pioneer' trees are dominant, through to a 'transitional' (mid-succession)

and later 'mature' (late-succession) stage where longer-lived and/or more shade-tolerant species become dominant (e.g. Hibbs 1983, Peterken & Jones 1987, 1989, Stephens & Ward 1992, Emborg *et al.* 2002). Although shade-tolerance and longevity are usually constant amongst individual species, growth performance is often dependent on the local species mixture and the soil conditions, topography and microclimate (e.g. Evans 1984, Botkin 1993).

A third, 'understorey reinitiation stage' (Oliver & Larson 1996) or 'biostatic phase' (Oldeman 1990) occurs in many situations. This usually happens after many decades of stem exclusion and is characterised by the development of an understorey of shade-tolerant shrubs and advance regeneration (Oliver & Larson 1996). It reflects changes in the vigour of canopy trees and a consequent increase in light and nutrients at the ground (e.g. Emborg 1998). This development represents a departure from the initial floristic composition and a shift to the relay floristics model of succession, i.e. the successive replacement of one group of species by another as a result of site modification (Egler 1954).

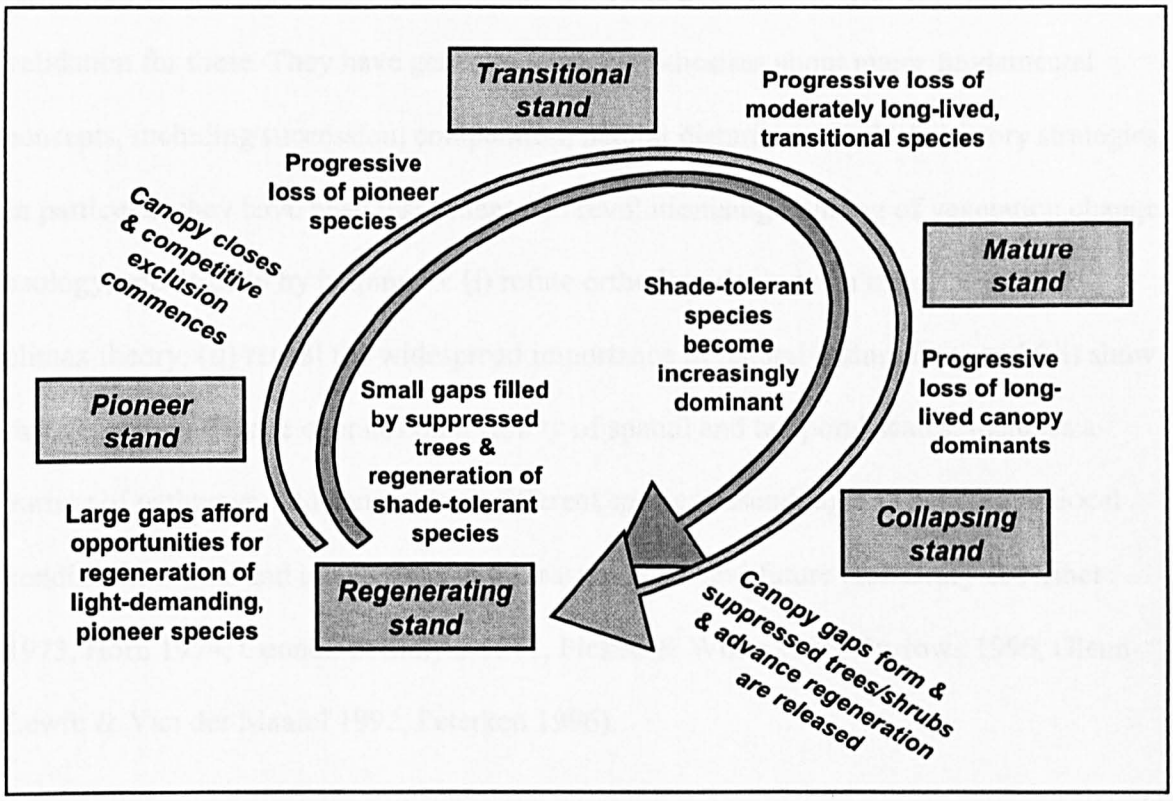
A final 'old growth stage' (Oliver & Larson 1996) or 'degradation phase' (Oldeman 1990) is reached later. During this the dominant canopy trees die off due to senescence, typically in an irregular fashion. The gaps created are usually filled by individuals already established in the understorey/sub-canopy and by new regeneration. Gradually a heterogeneous, mixed-aged woodland is created. Once this is complete the wood can be described as 'true old growth' as it is composed entirely of trees that have developed in the absence of allogenic (outside) processes. The term 'old growth' is also used more narrowly (see Helms 2004) to refer to structurally diverse stands with old trees, accumulations of dead wood, and a range of associated specialised organisms (e.g. Parker 1989). Because most temperate stands are affected by natural disturbance, the development of true old growth stands is uncommon. Dominant trees often die prematurely due to a combination of

senescence and natural disturbance and stress (notably wind- or ice-storms, drought, fire, disease and insect defoliation): die back and stand breakdown is sometimes rapid and large-scale (e.g. Mueller-Dombois 1986, Franklin *et al.* 1987, Everham 1996).

These changes can be conceptualised in an overall 'cycle of stand development' (Figure 1.1). Two major pathways can be envisaged depending if large or small gaps are created when stands break-up. Large gaps allow light-demanding pioneer trees to regenerate, whereas only relatively shade-tolerant trees are capable of regenerating in small gaps. The developmental stages or phases that occur during the cycle can be characterised by the size, structure and composition of the trees, the dominant processes that are driving stand development, and also by the progressive build-up of stand biomass. The number of pathways and stages, the composition and duration of each stage (and thus the overall length of the cycle), and the definition and terminology used varies between specific sites and studies. This is partly due to subjective choices made by individual researchers, but it also reflects real differences related to the complexity of the stands, site and disturbance regime. It is possible to map the spatial pattern of the developmental stages across a wood in a mosaic map (e.g. Emborg *et al.* 2002), which changes over time as each patch passes through the developmental cycle. The whole system has been referred to as a 'shifting mosaic-cycle' (Remmert 1991). It is possible that this reaches a perceived 'steady-state equilibrium' with the representation of each stage and biomass of the wood as a whole remaining relatively stable.

A major aspect of this study was to see how the cycle of stand development outlined above applied to near-natural woodland in lowland Britain. It was expected that similar developmental stages and major processes could be identified, given that the species mixture (or at least the genera present) and ecological conditions were not wholly dissimilar from other parts of the North Temperate Zone. Nonetheless, it was apparent that

Figure 1.1: General conceptual model of the overall cycle of stand development in natural temperate woodland. See text for full explanation. Based primarily on Bormann & Likens (1979), Leibundgut (1982), Mayer (1984), Průša (1985), Oldeman (1990), Remmert (1991), Korpeľ (1995), and Oliver & Larson (1996)



the outcome would be specific to the particular stands under study, and that certain factors would be more or less important, not least because of the effects of past-management and certain specific ecological conditions that exist in British woodland. Related to this, was the question of how would the relatively large-scale, even-aged, maturing stands that were inherited for study respond to natural disturbances and break-up under British conditions.

1.2.3. Value of studying natural stand development

Natural woodland is a valuable resource for scientific research, education, environmental monitoring, and as a reference to define and measure how far removed managed woods and landscapes are from natural (Peterken & Backmeroff 1989, Peterken 1996, 2000a).

Long-term studies of changes in natural woods (in addition to other phenomenon) have made a central contribution to basic ecological science (Likens 1983, Franklin 1989). They have been used to test concepts and predictions, and provide the most convincing validation for these. They have generated new hypothesises about major fundamental concepts, including succession, competition, natural disturbance and life-history strategies. In particular, they have been instrumental in revolutionising thinking of vegetation change ecology, specifically by helping to: (i) refute orthodox ideology on the succession-to-climax theory; (ii) reveal the widespread importance of natural disturbance; and (iii) show that vegetation change operates on a variety of spatial and temporal scales, includes a variety of pathways, and can produce different species-assemblages depending on local conditions, events and interactions in the past, present and future (see Drury & Nisbet 1973, Horn 1974, Connell & Slatyer 1977, Pickett & White 1985, Burrows 1990, Glenn-Lewin & Van der Maarel 1992, Peterken 1996).

Knowledge of stand development is fundamental to woodland ecology, as trees and shrubs dominate the above-ground biomass and dictate what conditions, processes, structures and habitats prevail (e.g. Packham *et al.* 1992). Studies of natural stand development and natural woodland in general form a crucial reference point for the management of woodland nature reserves and the application of nature-based forestry, which aims fundamentally to mimic features and processes found in natural woodland (see Bradshaw *et al.* 1994, Peterken 1996, 1999, Fries *et al.* 1997, Franklin *et al.* 2002, Kuuluvainen 2002a, 2002b). Although these approaches have been applied widely in woodland nature reserves, they have been scarcely incorporated into production woodland in Britain (Pryor & Savill 1986). In parts of central and east Europe, however, the use of natural species mixtures, cutting regimes that mimic natural structures and diversity, and restocking based solely on natural regeneration have long been advocated (Köstler 1956).

1.2.4. Approaches to studying natural stand development

The natural development of a stand, from initiation to break-up, can potentially take several hundred years, and involves a wide-range of factors operating at many scales. The study of natural stand dynamics therefore covers many disciplines. It combines observation and interpretation with knowledge of many aspects of plant ecology (e.g. autecology, physiology, herbivory, succession), and a general understanding of associated aspects of soil science, climate, environmental influences, woodland history/management, woodland mensuration and statistics. Since ecologists seek an immediate understanding to what is a long-term, complex process it is necessary to use a variety of approaches (see Hytteborn 1986, Burrows 1990, Glenn-Lewin & Van der Maarel 1992, Peterken 1996). At least seven different approaches can be recognised, as outlined below, which complement each other and allow an integrated understanding to evolve.

1.2.4.1. Permanent plots

Permanent plots allow stand dynamics to be observed directly by following changes in fixed, relocatable plots. They are typically recorded every decade in temperate forests and range from small square, circular or irregular plots to narrow belt transects and much larger plots, exceptionally covering whole reserves. Most permanent plot studies have focused on individual trees, typically mapping all stems above a minimum threshold and recording their growth, mortality and recruitment between surveys. Sometimes additional aspects have been included, such as tree seedlings, regeneration groups, stand structure, stand profile diagrams, canopy gaps, dead wood and uprooted trees (e.g. Faliński 1978, Runkle 1998, Saniga & Schütz 2001, Vrška *et al.* 2001), and even repeated photographs (e.g. Proctor *et al.* 1980, Fujita *et al.* 2003). Long-running permanent plots studies in temperate deciduous woodland exist in Europe, North America and Japan. Several European countries have established a formal series of research reserves based on permanent plots

(Diaci 1998, Parviainen *et al.* 1999). Nevertheless, few permanent plot studies have run for more than three decades (Table 1.1).

Table 1.1: List of temperate deciduous woodland sites in eastern North America and Europe where permanent plots have been used to study long-term natural stand dynamics. Includes sites with studies that have lasted for three decades or more (based on the date of the last reported recording)

Name of site(s)	Study length (years)	Associated publication(s)
Eastern North America		
Bartlett Experimental Forest	60	Leak & Smith (1996)
Cockaponset/Meshomasic Forests	60	Olson (1965), Stephens & Waggoner (1980), Stephens & Ward (1992)
Davis-Purdue Research Forest	60	Ward *et al.* (1996)
Arnot Forest	53	Fain *et al.* (1994), Volk & Fahey (1994)
Davis-Purdue Research Forest	50	Parker & Leopold (1983), Parker *et al.* (1985)
Heart's Content	50	Whitney (1984)
Cascade Head Experimental Forest	48	Harcombe (1986)
Black Rock Forest	40-42	Lorimer (1981)
Harvard Forest	38	Hibbs (1983)
Donaldson's Woods	30	Schmelz *et al.* (1975), Barton & Schmelz (1987)
Europe		
Wistman's Wood (UK)	76	Proctor *et al.* (1980), Mountford *et al.* (2001a)
Bialowieza (Poland)	57	Faliński (1986), Bernadzki *et al.* (1998)
Lady Park Wood (UK)	54-55	Peterken & Jones (1987, 1989), Mountford (1994, 1997), Peterken & Mountford (1995, 1996, 1998)
Draved Skov (Denmark)	50	Wolf (2002), Wolf *et al.* (2004)
Mionší, Boubín (Czech Republic)	42-46 [145*]	Řehák (1959) Vaněk (1990), Vrška *et al.* (2000, 2001)
Denny Inclosure/Wood (UK)	40-45	Mountford *et al.* (1999), Mountford (2001), Mountford & Peterken (2003), this study
Badín, Bujanov, Dobroč, Kašivárová, Kyjov (Slovakia)	38-47	Korpeľ (1995)
Clairinsh Island (UK)	37	Backmeroff & Peterken (1989), Mountford (2000b), this study
Huenstollen, Stoeberhai, Großer Freeden, Landwehr, Limker Strang (Germany)	30-34	Meyer (1995), Griese (1997), Meyer *et al.* (1999, 2000), Meyer (2004)

* at Boubín a 0.6ha plot established in 1851 was virtually relocated in 1961, though it remains unclear which of two alternative positions is correct

1.2.4.2. Stand characteristics

Stand measurements taken at one moment can be used to interpret the past development of natural stands. For example: Jones (1945) examined a range of size-class distributions measured in temporary plots in a range of temperate woods; Pigott (1975) examined the spatial pattern of regeneration and trees in plots in Bialowieza Forest; and Henry & Swan (1974) and Koop & Hilgen (1987) used traces of uprootings, fallen dead trunks and other

salient features to reconstruct the long-term dynamics of selected stands. Other studies have focused on canopy gaps characteristics (e.g. Barden 1981, Runkle 1998), made measurements of tree ring widths (e.g. Lorimer 1980, Rozas 2003) or tree ring counts (e.g. Peterken & Tubbs 1965), or recorded traces of fire and fraying scars (e.g. Zackrisson 1977, Mota & Nola 1996). Surveys of windstorm-damage in natural stands have revealed information about the factors that predispose stands to damage (e.g. Whitbread 1991, Foster & Boose 1992).

1.2.4.3. Chronosequences

A chronosequence approach implicitly substitutes space-for-time by comparing stands of different ages and assuming they differ mainly in terms of their age. For example, Korpel' (1995) used sets of profile diagrams and maps of developmental phases to study natural woodland development in central Europe, whilst Barkham (1978) mapped and measured the characteristic of different aged stands to develop a model of long-term dynamics in an oakwood in the uplands of south-west Britain.

1.2.4.4. Experiments/comparisons and research under semi-natural conditions

Experimental/comparative research can be an important tool in studying natural stand development and the factors associated with this. This includes controlled experiments that aim to mimic natural events, and comparisons between different 'natural' states. Examples of this approach include studies of artificial canopy gaps as made by Collins & Pickett (1987) and Clinton (2003), studies within and outside herbivore exclosures (e.g. Putman *et al.* 1989), and the famous Hubbard Brook comparison of undisturbed and manipulated stands in different watersheds (Bormann *et al.* 1970, Bormann & Likens 1979). Many aspects and factors controlling natural stand dynamics have been observed under semi-natural conditions. They include tree growth, mortality, physiology, seed production and

regeneration, herbivory, species autecology and natural disturbance. These can be used to interpret developments under 'natural' conditions and to parameterise computer models.

1.2.4.5. Mathematical modelling

Mathematical modelling can be been used to simulate natural stand dynamics by substituting components and processes with equations, and running them to project future composition. Validation is achieved by comparing the output against expected woodland composition or, rarely, against data from long-term plots (e.g. Lindner *et al.* 1997). Gap models have proved especially popular and particularly the JABOWA gap model developed for mixed deciduous woodland in eastern North America and the many versions developed from this (see Botkin 1993). More simplistic models based on transition probabilities have been used to predict the long-term species development of natural stands (e.g. Barden 1980, Stephens & Ward 1992).

1.2.4.6. Historical records

Historical records can be used to give an indication of the past state of a wood and its treatment. Such information has usually been used to compliment other stand measurements (e.g. Peterken & Tubbs 1965, Koop 1989).

1.2.4.7. Palaeoecology

Palaeoecology has been used to gain information on the long-term development of woodland (see Godwin 1975, Birks & Birks 1980). This approach involves using preserved pollen, charcoal and tree macrofossils. It can approximate former woodland vegetation and relate this to charcoal horizons, sedimentology, indicator plant species, climate and other factors (e.g. Bjorkman & Bradshaw 1996). Many palaeoecological studies are based on large-scale regional catchments, but some use sediments in small hollows that reveal more about local stand change (e.g. Iversen 1964). In some situations patches of sub-fossil trees

have been preserved and reveal remarkable insights into past dynamics (Allen 1992). Past woodland environments and interactions can similarly be assessed using mammal (e.g. Bradshaw & Mitchell 1999) or insect fossil evidence (e.g. Girling 1982).

1.2.4.8. Evaluation of each approach

Each of the above approaches can provide valuable information, but only of certain kinds and within certain spatial and temporal scales. There is a consensus that long-term permanent plot studies are an essential part of studying vegetation change and natural stand dynamics, particularly because they can: (i) provide a record of actual changes in vegetation; (ii) follow the demography of whole populations: (iii) observe the fate of individuals and connect cause with effect; (iv) detect casual, small-scale, short-term and unknown factors; (v) allow short-term patterns to be interpreted within a long-term perspective; (vi) help verify inferences from other approaches; (vii) generate new hypotheses based on the changes observed; and (viii) maintain up-to-date environmental surveillance (Austin 1981, Likens 1983, Franklin 1989, Magnuson 1990, Peterken 1993b, 1996, Bakker *et al.* 1996). However, permanent plot studies suffer because patience is needed to obtain results, the findings are sometimes of limited value or irrelevant to current ecological issues, there are methodological and practical issues to resolve, the inferences are often drawn by an ecologist who was not involved with the initiation of the observations and may not be privy to the original intentions, and the precise outcome is unpredictable. Long-term research of this type requires an open-ended approach and lends itself to post-hoc analysis and hypothesis testing only in the broadest of terms (Taylor 1989, Peterken 1993b, 2000b).

Stand characteristics and chronosequences can be readily observed, but both make implicit assumptions that may be invalid. Residues of past events can be overlooked or under-

estimated (Fox 1989), and the assumption of chronosequences that two sites have the same condition and history can be unreliable (Pickett 1989).

Experiments, comparisons and research conducted under semi-natural conditions often provide valuable information on the factors controlling stand dynamics. They can isolate cause-from-effect and avoid waiting for unpredictable natural events to happen. They can be a major source of information in regions where natural woodland and studies of them are scarce. However, such research is ultimately a substitute for studies in natural woodland, and care is needed extrapolating the results to such situations.

Modelling is a useful tool to help understand past and present vegetation dynamics and to predict future developments, but it is based on certain assumptions and often the outcomes are insufficiently validated.

Historical records provide some retrospective information, but records are usually incidental, imprecise and incomplete. Palaeoecology is the only source of information spanning thousands of years. However, fossil preservation is selective, availability of sites is restricted, and only small hollows provide information at the stand scale. Both of these approaches are time-consuming and results require careful interpretation.

In most situations it is advantageous to combine more than one of these approaches. For example, Koop (1989) used a combination of stand characteristics, historical records and palaeoecological information to reconstruct the long-term dynamics of several woods in lowland Europe, and Wolf *et al.* (2004) combined records of stand characteristics, 50-years of observations from two permanent plots, historical records and several fossil pollen records to demonstrate the long-term context and relations between recent and past-changes in an untreated, mixed deciduous wood in Denmark.

1.3. Natural woodland in lowland Britain

1.3.1. Phytogeographic position

The native woodland vegetation of lowland Britain belongs to the European temperate deciduous woodland biome (Jahn 1991). Similar biomes are found in parts of central and east Europe, eastern North America and the Far East (Röhrig & Ulrich 1991). Lowland Britain occupies part of the Atlantic phytogeographic province of north-west Europe. This stretches from north France to Denmark and shares many common features and environmental conditions. However, Britain is somewhat distinctive in that some major native tree species reach their natural limits within the country (with beech and hornbeam considered native only to southern Britain, whilst ash, birch, elm, field maple, hawthorn, hazel, lime, oak and others are native more widely), several woodland plant communities are rather different from their continental counterparts, and the climate is more markedly oceanic (Jahn 1991, Rodwell 1991, Peterken 1993a, 1996, Goudie & Brunsden 1994).

1.3.2. Surviving natural components

Woodland spread naturally across Britain after the last ice age ended around 12000 years ago, and at around 6-8000 years ago it covered much of the lowlands and contained a mixture of mainly deciduous species, notably hazel, lime, oak, alder, elm, birch and ash (Birks *et al.* 1975, Godwin 1975, Greig 1982, Bennet 1989, Rackham 2003). Thereafter, a great deal of the woodland cover was removed for agriculture and all surviving fragments were brought under regular management, mostly as coppice or wood-pasture (Rackham 2003, Peterken 1993a, 1996).

Although this means that no truly natural woodland survives today, many modern-day woods have inherited a range of features associated with the original-natural woodland of 6-8000 years ago and especially ancient semi-natural woodland (Rackham 2003, Peterken 1993a, 1996). This category of woodland covers about 1.5% of the land area and accounts

for about 11% of all British woodland (Spencer & Kirby 1992). It has retained a semi-natural composition because the original-natural stand mixture was (more or less) preserved and many species proved tolerant of coppice and wood-pasture management (Rackham 2003, Peterken 1993a, 1996). However, much of this woodland occurs in small, highly fragmented, isolated blocks of relatively uniform, young stands (Thomas *et al.* 1997, Kirby *et al.* 1998). Many features associated with old-growth woodland are scarce, notably a high degree of heterogeneity, large trees and abundant dead wood, and a range of saproxylic and epiphytic plants and animals and cavity-nesting birds (e.g. Harding & Rose 1986, Tomialojic 1991, Martin 1992, Peterken 1992, Kirby & Drake 1993, Newton 1994, Samuelsson *et al.* 1994, Boncina 2000, Ódor & Standovár 2001, Fan *et al.* 2003). In addition, all woodland in Britain lacks natural self-regulating populations of large carnivores and herbivores (e.g. lynx, wild cattle and boar) (Corbet & Harris 1991). Although the impact of large herbivores on the original-natural woodland is disputed (Buckland & Edwards 1984, Vera 2000, Peterken 2001, Bradshaw 2002, Svenning 2002, Bradshaw *et al.* 2003, Kirby 2003, Rackham 2003), there has no doubt been substantial alterations to the original-natural grazing regime, which has had knock-on effects on the flora and fauna in extant semi-natural woods (see Flowerdew & Ellwood 2001, Fuller 2001, Fuller & Gill 2001, Gill & Beardall 2001, Kirby 2001, Stewart 2001). Various non-native species have also colonised semi-natural woods in recent times, notably sycamore, American grey squirrels and Chinese muntjac deer (Corbet & Harris 1991, Peterken 1996, Selmes & Peterken 1997).

1.3.3. Concepts of natural woodland

The concept of natural woodland in Britain is rather ambiguous (see Peterken 1996, 2000b). First, it is possible to define several types of naturalness that are not only distinct in concept, but could have quite different compositions and dynamics. Thus, for example, the last of a sequence of original-natural woodland types in East Anglia were dominated

largely by lime, oak, hazel, ash and/or elm (Rackham 2003), but the woodland that would develop if left to natural processes indefinitely (future-natural) might well be dominated by sycamore, beech or hornbeam and lack oak and lime. In several minimum-intervention reserves such a change is seen as undesirable and unwanted species are actively cut out. Second, there is little doubt that, since the last glaciation, people have always had some influence on woodland, and continue to do so even in non-intervention reserves. Thus, most original- and future-natural woods are in a sense 'near-natural' if human impact is discounted as a natural factor – even if it is not, it is unclear what degree of human activity can be counted as natural. Third, there is considerable uncertainty about the composition and impact of large herbivores in original-natural woodland: some contend that in gaps there would be a prolonged 'parkland' stage with large herbivores delaying regeneration (Vera 2000), whilst others have assumed that gaps would regenerate largely unhindered and soon close (Peterken 1996). It is therefore unclear how large herbivores should be treated in modern- and future-natural reserves. Fourthly, the mammal fauna found in modern woods today includes certain species that were not present in original-natural woodland, but which can be seen as surrogates for original-natural species and as a natural component of modern- and future-natural woods (e.g. American grey squirrel, domesticated forms of wild cattle, ponies and pigs, exotic species of deer).

This study was firmly based on reserves whose composition was natural in the sense that the trees and shrub species were predominately those that were inherited from original-natural woodland. Although all the stands were predominately left untreated whilst under study, they had all been treated as either coppice or wood-pasture in the past, and most were to some degree influenced by large herbivores and other mammals, some of which were species alien to the British Isles. The implications are considered in the discussion.

1.3.4. Studies of natural woodland in lowland Britain

1.3.4.1. Studies of past-natural woodland

There have been many palaeoecological studies of the development of the natural woodland in Britain that reveal much about regional woodland development in pre-historic and later times. Most are based on pollen diagrams (e.g. Godwin 1975, Bennet 1986, Waller 1993). They show that the composition of woodland changed as successive tree and shrub species colonised and spread across the country, that over certain periods major species alternated in abundance indicative of the type of cyclical change shown in Figure 1.1, and that windthrow and Dutch elm disease were important disturbance agents (Allen 1992, Rackham 2003). Other aspects of the structure and dynamics of pre-historic woods have been extrapolated from studies of surviving semi-natural woods, natural woods in other countries and other sources (Rackham 1988, 1992, 2003, Peterken 1996, Vera 2000, Svenning 2002).

1.3.4.2. Studies of recent natural stand development

Recent natural stand change has been studied in British woodland using a combination of permanent plots, stand characteristics, chronosequences, historical records and experimental enclosures (Peterken & Backmeroff 1989, Peterken 1996, Hall *et al.* 1999). Important studies have been made in various minimum-intervention reserves (see Table 1.2), where secondary woodland has been allowed to develop by natural regeneration (Merton 1970, Peterken 1996), where the general characteristics recorded in extant ancient semi-natural woods have been assessed (Peterken & Tubbs 1965, Barkham 1978, Rodwell 1991, Peterken 1996, Green & Peterken 1997, Kirby *et al.* 1998, Rackham 2003), and where natural regeneration has studied (e.g. Watt 1919, 1923-25, Pigott 1983, Humphrey & Swaine 1997a, 1997b, Packham & Hilton 2002). These have revealed some information about: (i) the main characteristics and potential role of the main native trees and shrubs under (supposed) natural conditions; (ii) the major factors that affect aspects of stand

development and particularly natural regeneration (seed production, dispersal and predation, germination, establishment conditions, seedling growth, disease, damage by insects, small mammals and large herbivores); (iii) the main types and impact of natural disturbance; and (iv) the potential pathways, outcomes and structures associated with natural stand development.

Although many individual aspects of natural stand change have been studied (at least under semi-natural conditions), and the template presented in Section 1.2.2 appears to be broadly applicable, there nevertheless remains only limited guidance as to: (i) the general character of modern-day natural woods in lowland Britain; (ii) the full range of behaviour of the main native tree and shrub species and main native woodland types under natural conditions; (iii) the processes, structures and patterns that would prevail in natural reserves in Britain, especially in old-growth woodland; (iv) the types, importance and responses of stands to natural disturbance; (v) the role and effects of large herbivores and other biota; and (vi) the differences between natural and managed native lowland woodland and natural temperate woodland elsewhere. Moreover, there are few long-term permanent plot studies to validate extrapolations or speculation about natural woodland development.

In addition to addressing the issues listed above, this study also extended several permanent plot studies that contribute to an informal network of minimum-intervention research reserves, as developed by Peterken & Backmeroff (1989). Britain has never developed a formal set of such reference reserves, though many sites have been treated this way, deliberately or by default. Table 1.2 lists those in which 'permanent plots' of various kinds have been established, and the output of research publications. The oldest study, started in 1921, was not conceived as a long-term study, but developed when a descriptive plot was relocated and recorded. The earliest long-term plots to be started and sustained are in Lady Park Wood, with Denny Wood and Clairinsh (both of which were included in this

Table 1.2: List of sites in Britain where permanent plots have been used to study natural stand dynamics. Includes studies where the plots have been recorded at least twice

Study length (years)	Name of site(s)	Main species	Associated publication(s)
76	Wistman's Wood, Devon	Oak, rowan	Proctor *et al.* (1980), Mountford *et al.* (2001a)
54-55	Lady Park Wood, Gwent	Beech, ash, lime, oak, birch, hazel, elm	Peterken & Jones (1987, 1989), Mountford (1994, 1997), Peterken & Mountford (1995, 1996, 1998), Mountford & Peterken (1999)
40-45	Denny Inclosure/ Wood, New Forest	Beech, oak, holly	Mountford *et al.* (1999), Mountford & Peterken (2003), this study
37	Clairinsh Island, Loch Lomond	Oak, holly, rowan	Backmeroff & Peterken (1989), Mountford (2000b), this study
31	Ham Street Woods, Kent	Oak, hazel, hornbeam	Knott & Petley-Jones (1991), Thomas *et al.* (1994)
30	Colt Park Wood, Yorkshire Dales	Ash	None
25	The Mens, Sussex	Beech, oak, holly, ash	This study
24	Coed Cymerau, Snowdonia	Oak	None
17	Wytham Wood, Oxfordshire	Ash, sycamore, oak, hazel	Kirby *et al.* (1996), Kirby & Thomas (1999)
16	New Forest (ten sites)	Beech, oak, holly	Koop (1989), Siebel & Bijlsma (1998)
13	Ridge Hanger, Hampshire	Beech, ash	Mountford & Ball (2004)
11	Monks Wood, Cambridgeshire	Ash, hazel, field maple	This study
11	Noar Hill Hanger, Hampshire	Beech, ash	Mountford (2004), Mountford & Groome (2004)
10	Langley Wood, Wiltshire	Oak, hazel, lime, birch	This study
10	Scords Wood, Toy's Hill, Kent	Beech, birch, oak	This study
10	Dendles Wood, Devon	Beech, oak	Mountford *et al.* (2001b)
10	Craigellachie, Cairngorms	Birch	Mountford & Peterken (2000)
8	Buckholt Wood, Gloucestershire	Beech, ash	Mountford (2003)

study) lagging not far behind. Other important nearby minimum-intervention research reserves are found at: (i) La Tillaie and Le Gros-Fouteau (Fontainebleau, near Paris), which has stands that have been virtually untreated since 1372 (Pontailler *et al.* 1997); (ii) Hasbrucher and Neuenburger (near the north-west German coast), which contains impressive areas of derelict wood-pasture (Koop 1981); and (iii) Białowieża Forest (eastern Poland), which has a 5000ha, near-natural core area (Faliński 1986). Nonetheless, most minimum-intervention reserves in north-west Europe (as in Britain) have been only recently set aside after many centuries of management. Only by travelling into the Carpathian-Balkan mountain ranges of east-central Europe and to eastern North America

can a concentration of near-virgin reserves be found, though the composition and conditions associated with these are significantly different from in Britain (Peterken 1996).

Recent efforts to increase the number of recorded sites have culminated in the publication of a provisional series of representative reserves for England and proposals for recording therein (Mountford 2000a, Peterken 2000a). Indeed, over the last two decades there has been a growing interest in restoring natural woodland reserves in Britain (Peterken 1991, 1993a, 1996, Kirby & Rush 1994, Forestry Commission 1998). Many nature reserves now include areas dedicated to minimum-intervention and there has been a substantial increase in the use of natural regeneration and interest in other nature-based silvicultural treatments (e.g. Kerr 1999). This trend is apparent in other Europe countries (see Broekmeyer & Vos 1993, Parviainen *et al.* 1999). Nevertheless, no further development has been made to formalise a series of reference sites for Britain and, as in other long-term studies, it continues to prove difficult to maintain existing baselines with initiators and associated institutions having lost interest, records having not been properly archived, and financial support proving difficult to source (Peterken & Backmeroff 1989, Peterken 2000b).

2. RATIONALE AND METHODOLOGY

2.1. Rationale

The broad aim of this study was to increase our understanding of stand development in near-natural woodland reserves in lowland Britain, and present a first synthesis on this subject. Considering the review of the current state of knowledge and research approaches (as presented in Chapter 1), it was decided that this would be achieved best by adopting the following research objectives:

1. To re-record a selected number of permanent plot studies and make a detailed examination of the patterns and causes of stand change – this would add to the limited number of other sites studied in this way (see Table 1.2), and expand the knowledge base and make it more comprehensive and representative;
2. To expand the recording method applied at the study sites – this would establish some common variables, allow for comparison between sites, and also make the knowledge base more comprehensive;
3. To combine the new findings with those from other relevant studies – this would maximise the knowledge base from which a general synthesis could be made.

There were three main constraints to achieving this: (i) the scope of the work was to develop a general synthesis rather than test an hypothesis through an experimental approach – thus, the approach to data gathering had to be general rather than specific, which presented some difficulties in deciding precisely what to record; (ii) the permanent plot studies available for re-recording, what they represented, the features of interest, and baseline records were predetermined by earlier researchers, and there was no control over what natural events had taken place since the plots were established; and (iii) the time available for recording was limited by financial resources to pay for accommodation and

travel costs, the availability of volunteers to help with fieldwork, and the ease with which sites could be accessed and traversed.

Accepting the above constraints, the following working objectives were decided upon in terms of which sites and what field recording were included:

1. To focus on specific sites that had adequate baseline records and represented a range of lowland native woodland types, at various stages of stand development and with various features of interest – this would ensure a reasonably broad and representative coverage;
2. To focus on recording general changes in the stand composition and structure and the causes behind this – this was fundamental to the quantification and interpretation of the general development of the stands and the impact that disturbances had;
3. To be expedient and adaptive and ensure that key aspects, especially features and processes that were well-represented at one site and/or were not apparent or only partially recorded elsewhere (e.g. windstorm-damage), were included so that the final overview was as far as possible comprehensive and supported by actual observations;
4. To make best use and build on the inherited methodology and records of individual trees/features, as more would be learnt from tracking the fate of individual features recorded in the past than by starting anew;
5. To develop existing methodologies towards a standard format, which was scientifically robust, recorded features of actual and potential interest, and had or could be applied at similar sites to allow for comparison (following Mountford 2000a).

Although permanent plots formed a major component of the research, it was recognised that it was a priority to incorporate other approaches where available and appropriative. In

particular, an interpretation was made of the stand characteristics recorded when the plots were first established, which considerably extended the time period over which stand development could be determined at each study site and allowed past changes to be related to recent (observed) changes and vice versa. In addition, available chronosequences and historical records were used if they were available, and other experimental/comparative research, studies made under semi-natural conditions, and other types of research were used to interpret the stand development recorded and to support the overall synthesis.

2.2. Methodology for new recording

2.2.1. Study sites selected

Table 2.1: Summary details of the six study sites, including their coordinates, vegetation, main soils and elevation. See also Figure 2.1 and Table 2.2

Site name	Coordinates Grid reference	Main woodland type present Equivalent type in the NVC [a] Main tree/shrub species	Main soils [b] Height above sea level
Denny Inclosure	50.8°N, 1.5°W SU 3306	Southern beechwood W14/15 *Fagus sylvatica-Rubus fruticosus/Deschampsia flexuosa* woodland Beech, oak, holly	Typical stagnogley 30m
The Mens	51.0°N, 0.5°W TQ 0223	Southern beechwood W14 *Fagus sylvatica-Rubus fruticosus* woodland Beech, oak, holly, hawthorn, hazel	Typical stagnogley 35m
Toy's Hill	51.2°N, 0.1°E TQ 4752	Southern beechwood W15 *Fagus sylvatica-Deschampsia flexuosa* woodland Birch, beech, oak, holly	Typical paleo-argillic brown earth 200m
Monks Wood	52.3°N, 0.2°W TL 2080	Southern ashwood W8 *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland Ash, oak, field maple, hazel, hawthorn	Typical calcareous pelosol 20m
Langley Wood	50.9°N, 1.7°W SU 2220	Southern oakwood W10 *Quercus robur-Pteridium aquilinum-Rubus fruticosus* woodland Oak, birch, lime, hazel, hawthorn, ash	Typical stagnogley 50m
Clairinsh	56.1°N, 4.6°W NS 4189	Northern oakwood W11 *Quercus petraea-Betula pubescens-Oxalis acetosella* woodland Oak, birch, holly, rowan, hazel, alder	Typical/stagnogleyic brown earth 10m

[a] based on the National Vegetation Community types in Rodwell (1991); [b] based on information from the Soil Surveys of England, Wales & Scotland and Mackney *et al.* (1983)

Six sites with permanent plots were selected for re-recording for this study. The location, summary details, features of interest and recording of these are given in Tables 2.1-2 and Figure 2.1. All were at relatively low altitudes, though Clairinsh was located in north-west Britain, whereas the other five sites were in southern England. Three sites were composed

predominantly of mixed beech woodland, one was mixed ash woodland, and the other two were mainly mixed oak woodland. Two sites (Langley, Clairinsh) contained distinctive areas of wet woodland. They were all designated as Sites of Special Scientific Interest.

Figure 2.1: Location of study sites. See Tables 2.1-2 for other details

Table 2.2: Features of interest and summary of the records made at each study site

Site name	Main stand characteristics and features of interest to this study	Years of main records	Number of trees on record*	Dimensions of permanent plot(s)	Main features recorded
Denny Inclosure	Ex-wood-pasture developed into high forest with abundant regeneration and a range of older trees dating from enclosure in 1870; records of stand condition about nine decades later and of stand change over next four decades during which deer and pony browsing, drought, windstorms and grey squirrels impacted	1956 1958/9 1964 1984 1988 1996	2421	Single, 1km long, 20m wide, belt transect set up in 1956-8/9 (maximum area recorded = 1.92ha)	Location, species, dbh/gbh and status of live trees/shrubs; location of low-growing (holly) scrub; and (mainly at last recording) condition of live trees/shrubs; location, condition and abundance of snags and fallen logs; location of established seedlings, uprooted trees, canopy gaps, and main ground vegetation patches
The Mens	Ex-wood-pasture developed into high forest with abundant regeneration and a range of older trees dating from enclosure in about 1850; records of stand condition about 120-130 years later and of impact and response to localised windstorm-damage over next decade	1972/4 1987/8 1998	3715	A. Twelve, 20m diameter, circular plots set up in 1988 (maximum area recorded = 0.38ha) B. Nine, 115-1090m^2, canopy gap plots set up in 1987 (maximum area recorded = 0.42ha)	A. Location, species, dbh/gbh, and status of live trees/shrubs; and (mainly at last recording) condition of live trees/shrubs; location, condition and abundance of snags; location of established seedlings, uprooted trees, canopy gaps and main ground vegetation patches B. Extent of canopy gaps; location, species, status, dbh/gbh and condition of all live trees/shrubs and uprooted/broken large individuals in and around the gaps; focusing initially on individuals attaining 3m height, and at last recording on large trees, sapling trees attaining 1.3m height, and established tree seedlings, the condition of trees/shrubs, and the location of dense shrubby growth and main ground vegetation patches Also, abundance and condition of fallen dead wood in compartment
Toy's Hill	Ex-wood-pasture developed into high forest dating from enclosure in about 1850, but was virtually levelled in 1987 windstorm and regenerated strongly; records of stand condition about 140 years later and of impact and response to severe windstorm-damage over next decade	1988 1992 1998	1112	Single, 97m long, 20m wide, belt transect set up in 1988 (maximum area recorded = 0.19ha)	Location, species, dbh/gbh, status, and condition of live trees/shrubs, uprooted trees, snags and fallen logs; location of surviving tree canopy; and (mainly at last recording) location of recruits, established tree seedlings and main ground vegetation patches
Monks Wood	Ex-coppice site developed into high forest with abundant regeneration and a scatter of older oak standards dating from last felling about 1920; records of stand condition about seven decades later and stand change thereafter over next decade during which deer browsing and windstorms impacted	1985 1996	9859	Four, 180-270m long, 20m wide, belt transects set up in 1985 (maximum area recorded = 1.70ha)	Location, species, dbh/gbh and status of live trees/shrubs, uprooted trees and snags; location of established seedlings; and (mainly at last recording) condition of live trees/shrubs; abundance and condition of snags and fallen logs; and location of fallen logs and canopy gaps

Continued overpage

Table 2.2 continued

Site name	Main stand characteristics and features of interest to this study	Year of main records	Number of trees on record*	Dimensions of permanent plot(s)	Main features recorded
Clairinsh	Ex-coppice site developed into high forest with range of retained standards, stored trees, and regeneration dating from last cutting in 1913; records of stand condition about five decades later and of stand change over next four decades during which windstorms impacted	1961 1986 1998	4190	Two, 174m/362m long, belt transects starting at 10m width in 1961 and increased to 20m width in 1986 (maximum area recorded = 1.00ha)	Location, species, dbh/gbh and status of live trees/shrubs, uprooted trees and snags; and (mainly at last recording) condition of live trees/shrubs; location, condition and abundance of snags and fallen dead wood; location of established seedlings and canopy gaps
Langley Wood	Ex-coppice site developed into high forest with abundant regeneration and a scatter of older oak standards dating from last felling in about 1940; records of stand condition about five decades later and of stand change over next decade during which windstorms impacted	1986 1996	5814	Two, 273m/365m long, 20m wide, belt transects set up in 1986 (maximum area recorded = 1.28ha)	Location, species, dbh/gbh and status of live trees/shrubs, uprooted trees and snags; and (mainly at last recording) condition of live trees/shrubs; abundance and condition of snags and fallen dead wood; location of established seedlings, large fallen logs, and canopy gaps

* includes live stems/individuals/seedlings and dead snags/fallen logs

The study sites were selected because: (i) they contained features of interest to the study aims: (ii) they had permanent plot records that represented some of the best national (even international) studies of this type, including two of the longest running studies in Britain (going back to the 1950s/60s) and several later baselines established in the 1970/80s as part of the development of this field of research (see Peterken & Backmeroff 1989); (iii) the records covered a substantial area or number of trees, were of sufficient quality/detail, and in some cases had been recorded on two or more occasions; (iv) the records provided information on stand development in a range of widespread native woodland types, which had undergone various types and intensities of past felling, and now represented various stages of development with various degrees and types of development, recent disturbance and browsing; and (v) they were all relatively natural, being ancient semi-natural woods that had been managed by minimum-intervention for several or many decades.

2.2.2. Recording methods

A summary of the general methods and records made at each site is given in Tables 2.2 and 2.3. Further details are given under the individual site sections. At each site, one or more repeated recordings were made within a single or series of permanent plots/transects. These were marked in the field with metal or wooden stakes to allow for relocation. A range of features was recorded within the plots/transects. Although a general methodology was applied and several standard measurements were made, the specific dimensions and area of the permanent plots, the type and degree of detail recorded, and the repetition of measures made at each site differed considerably. Nevertheless, the primary feature recorded at all sites was the position and species of all live trees and shrubs that attained 1.3m tall. This (and many other aspects of the recording) were transferred or directly written onto scale charts (usually of about 1:100 scale) (see Figure 2.2a and 2.2b).

Table 2.3: Details of the recording methodology applied within the permanent plots/transects at the study sites. Not all the features were recorded at every site and on every occasion. Table 2.2 lists the main features recorded at each site. Full details of the records made are given Sections 3.1-3.6

Feature recorded	Methodology
[1] Position of trees/ shrubs and established seedlings	• Measured to an accuracy of about 10cm using standard tapes and basic geometry and mapped onto scale charts – the approximate position of additional stems on multi-stemmed individuals was sketched to allow relocation – some individuals located just outside the plots were included
[2] Species of tree/shrub	• Determined by leaves, bark, buds, etc. – sometimes the species of dead individuals could not be identified
[3] Gbh or dbh (girth or diameter of stems) taken at breast (1.3m) height	• Measured to the nearest cm or half-cm with a tape – the main stem and (usually) all additional live stems and forks and trunk shoots that arose below 1.3m height were included down to a minimum size threshold (typically 3-5cm gbh)
[4] Status of each stem/individual	• Stems/individuals were classed as either: alive (=with live leaves above 1.3m up); alive at the base only (=with live leaves but only below 1.3m up); or dead (=at least 1.3m tall and dead or alive at base only) – the following were also distinguished: standing and fallen individuals/stems; snags (=standing dead stems) and logs (=fallen dead stems); and established seedlings (new live individuals attaining 30-<130cm tall and several years age)
[5] Condition of stems/individuals	• In early recordings this was usually done only briefly and incompletely (e.g. 'crown-dead' stems were noted) – in the latest recordings this was done in more detail and more completely, usually by either classifying and/or describing for each stem the crown position, crown size, foliage condition, vigour, degree of die back and new growth, the cause of decline/damage/death, the amount of debarking or other damage, the general shape and branching pattern, and the height/decay state of snags • Crown position was usually classified as: *canopy* = in uppermost layer and not overtopped, *sub-canopy* = just below and mostly overtopped by canopy layer, or *understorey* = below sub-canopy layer (sometimes a *ground* layer was recognised where the crown was mainly <2m in height) • Crown size usually classified as: *very large* = crown spread above about 10m diameter, *large* = 6-10m diameter, *medium* = 3-5m diameter, *small* = 2m diameter, or *very small* = <1m diameter (adjustments were made where the foliage was thin or the crown had suffered major die back or branch loss) • Crown die back (which took into account loss of foliage due to all causes) was usually classified as: *very severe* = ≥90% crown loss, *severe* = 60-90% loss, *moderate* = 30-60% loss, or *part* = <30% loss • Grey squirrel and other mammal debarking damage was classified following the method adopted by Mountford 1997: *no damage* = no bark removed; *limited damage* = one or only a few small (<10% of circumference) patches debarked; *moderate damage* = one large (>50% of circumference) or a few medium (10-50% of circumference) or many small patches debarked; *severe damage* = two or more large or several medium and many small patches debarked; *very severe damage* = as for severe but with main stem ring-barked or much of crown snapped out/killed off – this included all old and fresh damage, using binoculars to view damage high up, and recording damage separately for the lower trunk (<2m height) and upper trunk (>2m height) • General shape, condition and cause of decline/damage/death were described in shorthand notes, either in a brief or more detailed form • Snags were usually assessed in four ways: (i) snag height was usually measured to the nearest 0.1m if <2 m height and estimated to nearest 0.5m if <5m height and nearest m if >5m height; (ii) snag decay was classified as: *solid* = no signs of decay, *part-rotten* = limited signs of decay, *rotten* = decay advanced, or *very rotten* = decay advanced and fragile to handle; (iii) the percentage remaining bark was estimated to the nearest 10%; and (iv) the abundance of remaining crown branches was noted
[6] Amount/condition of fallen dead wood	• Measured using the line transect method described by Warren & Olsen (1964) and Kirby *et al.* (1998) – this involved laying out a set of equal-length line transects (either within the study plot(s) or across the surrounding minimum-intervention compartment) and then measuring the diameter or girth (to nearest cm) of fallen dead stems ≥5cm diameter where they crossed the line • Alternatively or additionally, all larger pieces of fallen dead wood (≥10-15cm diameter and ≥1-2m length) within the plots were mapped (using method [1]) and the diameter and length measured with tapes • In both cases the original species was identified and the state of decline/decay assessed (as was done with snags under [5])
[7] Extent/origin/under-filling of canopy gaps	• The vertical projection of canopy gaps as viewed from the ground was approximately mapped onto the scale charts (from [1]) – notes were made on their origin and the degree of understorey infilling
[8] Additional salient features	• These were added to the scale charts (from [1]) and included things like: the orientation of leaning and fallen stems; patches of low-growing (holly) scrub or ground vegetation; and windthrown trees, root plates, banks, tracks and paths
[9] General aspects	• Photographs and descriptive notes about the plots

Figure 2.2a: Example of a transect chart. The diagram shows the chart for the right-hand side of transect I, section 3, 80-90m along in Langley Wood, as recorded by Christa Backmeroff in 1986. It is a bird's-eye view and shows the position and species of each individual (L = small-leaved lime, Qp = sessile oak, Ca = hazel, B/Bpub = birch, Fr = ash, Cm = Hawthorn) and the size (cm, gbh) of each stem. There were several lime and hazel coppice stools, a large oak standard, and some small birch, ash and hawthorn. Filled circles were standing dead stems (snags). A bank-and-ditch feature crossed the area

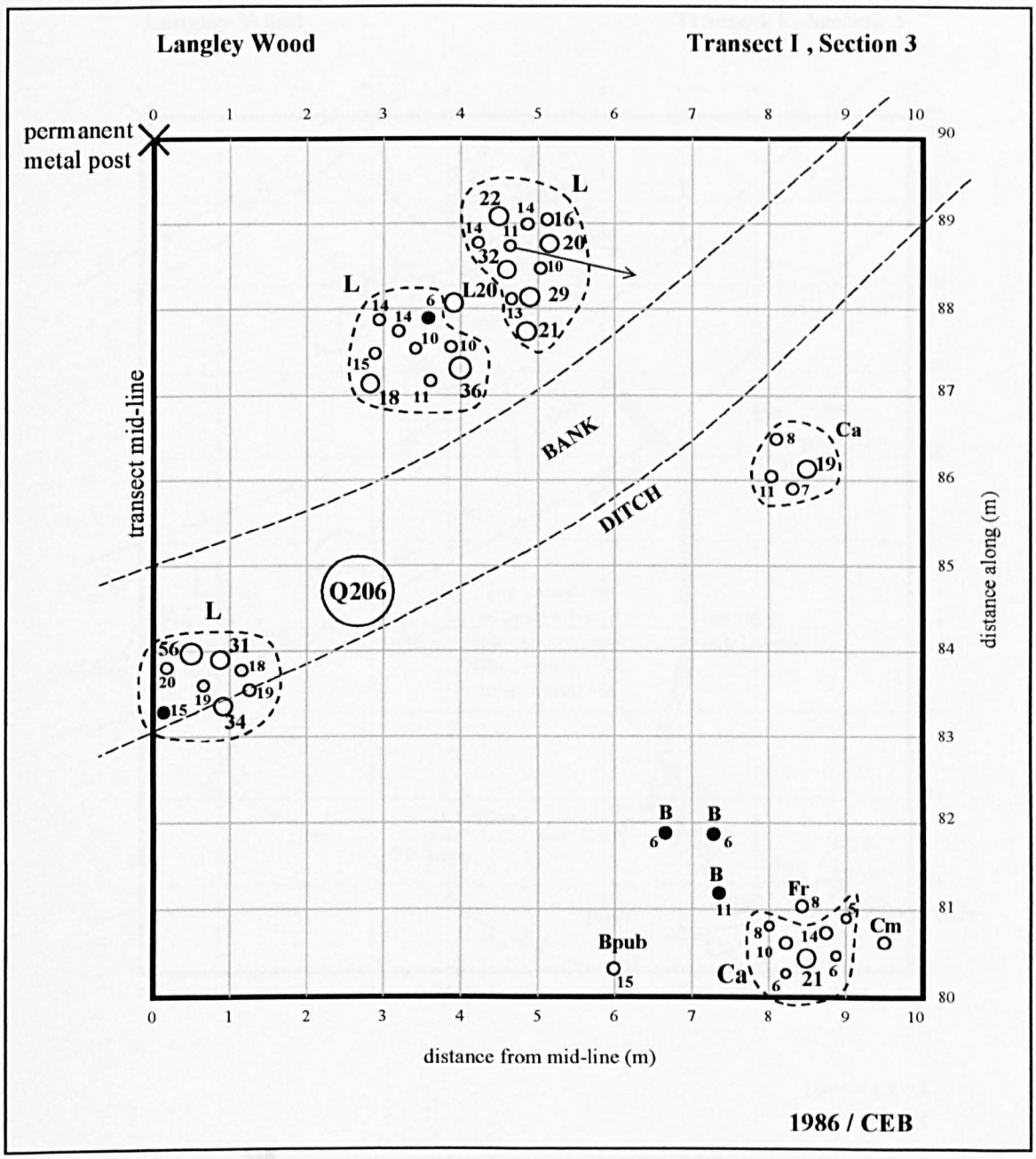
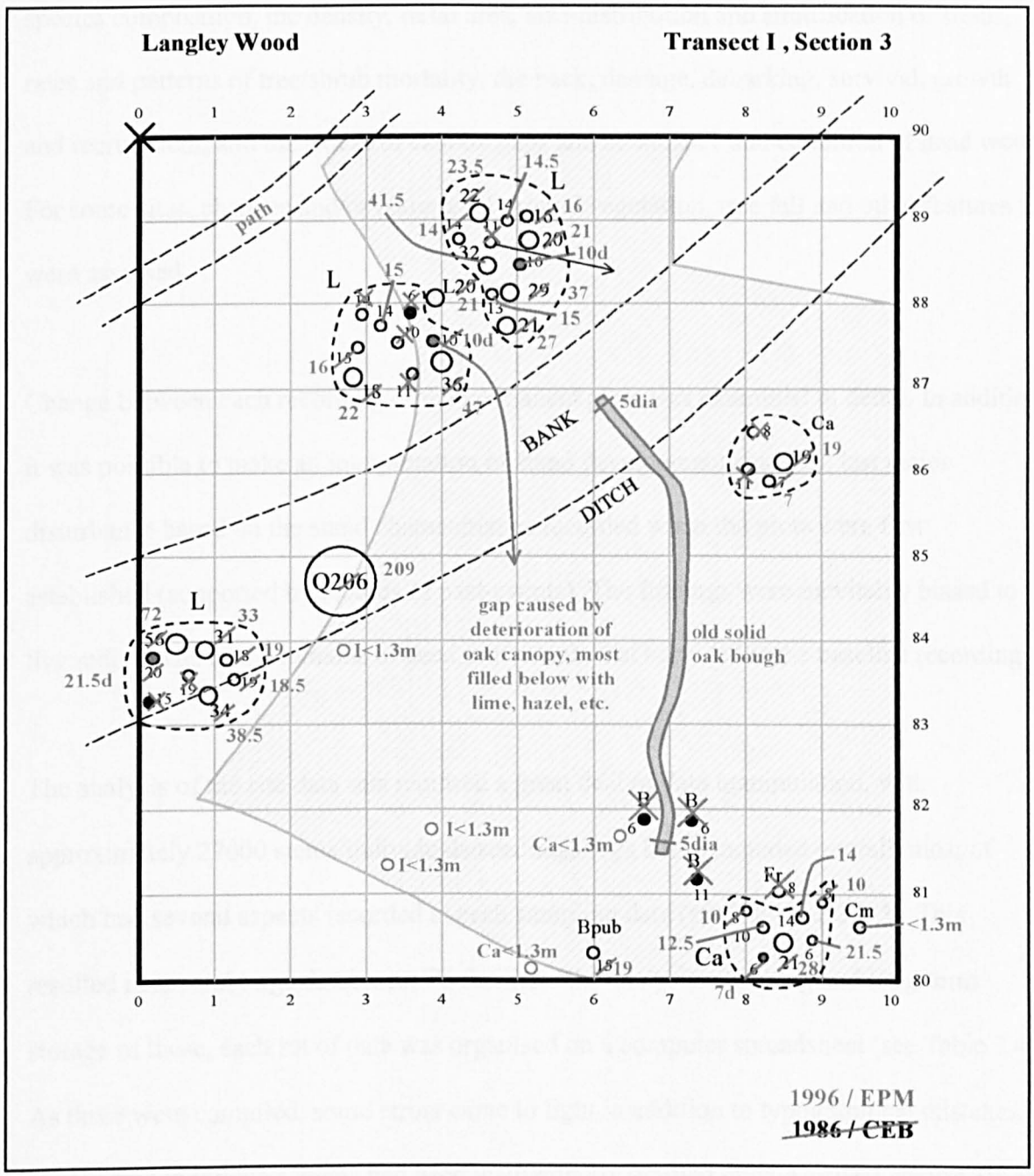


Figure 2.2b: Repeat of Figure 2.2a with the 1996 records overlain in grey. These show: (i) the size (cm, gbh) of stems; (ii) stems that formed snags (filled circles); (iii) stems that had died and collapsed (crossed out); (iv) several established seedlings of holly (I) and hazel (Ca), <1.3m tall; (v) the area below covered by a gap in the canopy (grey hatch); and (vi) a fallen dead oak branch with the end diameters. Part of the corresponding spreadsheet for this area is shown in Table 2.4.



2.2.3. Data analysis

The analysis focused on quantifying the structure and composition of the stands and how this changed over time. Some analyses were done across all sites, but others were targeted towards a specific feature or process at a particular site or sites. They focused on the species composition, the density, basal area, size-distribution and stratification of stems, rates and patterns of tree/shrub mortality, die back, damage, debarking, survival, growth and recruitment, and the extent of canopy gaps and abundance and condition of dead wood. For some sites, changes and/or patterns of ground vegetation, tree fall and other features were assessed.

Change between each recording of the permanent plots was examined in detail. In addition, it was possible to make an interpretation of stand development since the last major disturbance based on the stand characteristics recorded when the plots were first established (supported by records of past-events). The findings were inevitably biased to live individuals or the remains of dead individuals that survived at the baseline recording.

The analysis of the site data sets required a great deal of data manipulation, with approximately 27000 stems/individuals/seedlings/logs being included overall, most of which had several aspects recorded at each sampling date (see Tables 2.2-2.3). This resulted in several large databases. To facilitate the analysis, checking and long-term storage of these, each set of data was organised on a computer spreadsheet (see Table 2.4). As these were compiled, some errors came to light in addition to typographical mistakes. First, a few individuals/stems had been inadvertently omitted or categorised incorrectly at particular recordings. These errors were corrected based on available evidence and (where girth/diameter values were missing) by estimating the size from the increment rate of nearby properly recorded individuals. Second, a few trees decreased or increased in girth/diameter between recordings by implausibly large amounts. These were adjudged to

Table 2.4: Example of part of the spreadsheet for Langley Wood. This contains the permanent transect records from 1986 and 1996. Each row represents a stem and each column an attribute. The stems here are numbers 1015-1024. They come from part of transect I, section 3, and are included in the diagrams shown in Figures 2.2a/b. They include: an eight-stemmed, small-leaved lime (L), which had the largest stem increase from 56cm to 72cm gbh and two small stems die off (one of which persisted as a 4m tall, severely rotten snag); a holly (I) recorded as a short, established seedling in 1996; and a large, ex-standard, oak (Qp) that survived but with very severe die back (VS) and only a small crown (S) in the (upper) canopy (C)

										1986			1996										
Number	Transect	Section	Quadrat	Stems outside transect	Distance from left (m)	Distance from start (m)	Species	1996 stool code	Species/stem Code	Gbh (cm)	Status	Stool status	Gbh (cm)	Status	Stool status	Canopy position	Crown size	Crown die back	Debarking	Description	Snag length (m)	Snag decay	Snag bark (%)	Snag branches/twigs
1015	1	3	TR		10.7	83.7	L		19.00	56.0	1	1	72.0	1	1	C	S	P		Erect stem that has pushed through canopy oaks to emerge as strong competitor				
1016	1	3	TR		10.7	83.7	L		19.01	31.0	1		33.0	1		U	M	P		Stem arched over to W below lower oak boughs				
1017	1	3	TR		10.7	83.7	L		19.02	18.0	1		19.0	1		G	S	D		Stem leaning at 45 degrees to NW; part-covered in honeysuckle				
1018	1	3	TR		10.7	83.7	L		19.03	19.0	1		18.5	1		U	S	D		Erect forking stem mainly spreading to NW; much suppressed				
1019	1	3	TR		10.7	83.7	L		19.04	34.0	1		38.5	1		U	M	P		Stem leaning and spreading to N with arching branches; overtopped				
1020	1	3	TR		10.7	83.7	L		19.05	19.0	1			2										
1021	1	3	TR		10.7	83.7	L		19.06	15.0	2			2										
1022	1	3	TR		10.7	83.7	L		19.07	20.0	1		21.5	2						Dead snag killed by competitive exclusion	4	Solid, but with rotting base due to historical damage	100	Few branches
1023	1	3	TR		12.8	83.9	I		11.00					3										
1024	1	3	TR		12.8	84.7	Qp		13.00	206.0	1		209.0	1		C	S	VS		Erect standard forking into broad spreading crown from 5m up; loss of crown boughs and many branches with extensive die back; existing foliage very thin; clearly a failing tree that looks like it will die; little ivy present				

be mistakes made during measuring or recording and were also corrected by substituting interpolated values. Stems that decreased by only small amounts (which were generally infrequent) were not adjusted for. Instead these were accepted as being real shrinkages (due to bark loss or internal decay) and/or due to changes in recording methodology (from diameter to girth) or inconsistencies in recording (e.g. measured in different position, size rounded up or down, etc.).

Various parameters were calculated and statistical tests performed as detailed in Table 2.5. They were carried out following the advice given Hamilton (1975), Zar (1984), Sheil *et al.* (1995) and Kirby *et al.* (1998). All calculations and tests were performed using Microsoft Excel (version 7.0a) or Minitab (release 12.1) computer packages. The use of parametric and nonparametric tests depended on the normality of the data sets as viewed in histograms. Parametric testing was preferred where these showed an approximate normal distribution. Data sets were sometimes normalised using the log-transformation $x' = \log_{10}(x+1)$ (Zar 1984, p.238-9). Nonparametric rank testing was used for non-normal data.

Table 2.5: Parameters, types of statistical analysis and tests, and methods of calculation used in this study

Parameter/ type of analysis	**Calculation/use**
Stem diameter (dbh), girth (gbh), basal area (ba) at breast height	Calculated using basic geometry and assuming stems were circular in cross-section (dbh = gbh/π; ba = πr^2) (Hamilton 1975). The basal area (=cross sectional area of stems at height of measurement) was calculated as an estimate of total stem biomass (White 1981)
Mortality rate	Calculated using the true annual mortality rate (m) formulae as recommended by Sheil *et al.* (1995); where $m = 1-(N_0/N_1)^{1/t}$; N_0 and N_1 are population counts at the beginning and end of the recording interval t; included stems that died or were reduced to alive only at the base between recordings
Parametric regression analysis	Used to examine the relationship between the increment rate and initial size of stems (Zar 1984, chapters 17 & 21). Only stems that remained alive and upright at the end of each period and whose size was not interpolated for errors (see above) were included. The increment rate was calculated as the average annual increase by dividing the change in size by the number of growing seasons between each recording. The increment rate (dependent variable) was then related to the initial stem size (independent variable) using regression analysis. Some data were lognormal transformed before testing (Zar 1984, p.285-9). As it was expected that these regression lines might take a linear or a curved form, both the simple ($y = b_1x + a$) and quadratic ($y = b_2x^2 + b_1x + a$) forms of the equations were examined (Zar 1984, p.263-8, 361-7). If the additional quadratic term proved significant, then this form of the regression was selected as the best-fit. The significance of the regressions and additional quadratic term was determined using analysis of variance. In addition, the coefficient of determination (r^2) value was presented, as this showed how much of the total variation was accounted for by the fitted regression (Zar 1984, p.271)
Nonparametric type of analysis of variance (ANOVA)	Used to determine the significance of differences between the average rank increment rates for stems in different crown position/size categories, where more than two sets of data were being compared (k>2). This involved using an overall single factor Kruskal-Wallis ANOVA by ranks (H) test (adjusted for tied ranks) (Zar 1984, p.176-9), and subsequent Tukey-type multiple comparisons (Q) tests to pinpoint which pair-wise comparisons differed significantly (Zar 1984, p.199-201). The Mann-Whitney two-sample rank (U) test (adjusted for tied ranks) was used for the same purpose when only two sets of data were being compared (k=2) (Zar 1984, p.138-41)
Parametric paired-sample (t) test	Used to determine the significance of the difference between the average values of repeated measurements of basal area, stem density, and stem increment rates made within the same transect sections (Zar 1984, p.150-2)
Nonparametric Spearman rank correlation (r_s) test	Used to determine the significance of correlations between the basal area/density of stems in individual transect sections, and between the increment rates achieved by stems in different periods (Zar 1984, p.318-20). The test was adjusted for tied ranks

Continued overpage

Table 2.5 continued

Parameter/ type of analysis	**Calculation/use**
Nonparametric chi-square analysis (χ^2)	Used to test the significance of associations between stem frequency counts as constructed in contingency tables (Zar 1984, chapter 6). This included counts of stem numbers in various debarking, crown die back, crown position, crown size, dbh, and dead wood decay classes
Fallen & standing dead wood volume and length	Calculated in different ways depending on the sampling method. Where line-transects were used to estimate fallen dead wood, the volume (V_{fdw}) and length (L_{fdw}) were derived using the equations given by Kirby *et al.* (1998): $V_{fdw} = \Sigma(\pi^2 d^2/8L)$ ($m^3\,ha^{-1}$); $L_{fdw} = (\pi N/2L) \times 10000$ ($m\,ha^{-1}$), where L = total length (m) of the transects, N = number of stems measured, d = diameter (cm) of each stem. Otherwise, snag (=standing dead wood) volume (V_{snag}) was calculated from girth/diameter (g/d) and height (h) measurements, assuming snags were circular in cross section and cylindrical in shape, and using basic geometry ($V_{snag} = \pi d^2 h/4$) (Hamilton 1975). This seemed reasonable for snags of a few metres height, but probably over-estimated the actual volume of taller snags, albeit that remaining side branches reduced this effect. Fallen dead wood volume was calculated in a similar fashion when using the measurements of larger logs. From the mid-diameter (md) and length (l) measurements, $V_{fdw} = \pi d^2 l/4$ (volume of cylinder), whilst from the base-diameter (bd) and end-diameter (ed) measurements, $V_{fdw} = \pi l(bd^2 + bd.ed + ed^2)/12$ (volume of cone frustum) (Hamilton 1975)

3.1. Stand change and natural disturbance at Denny Inclosure

3.1.1. Introduction

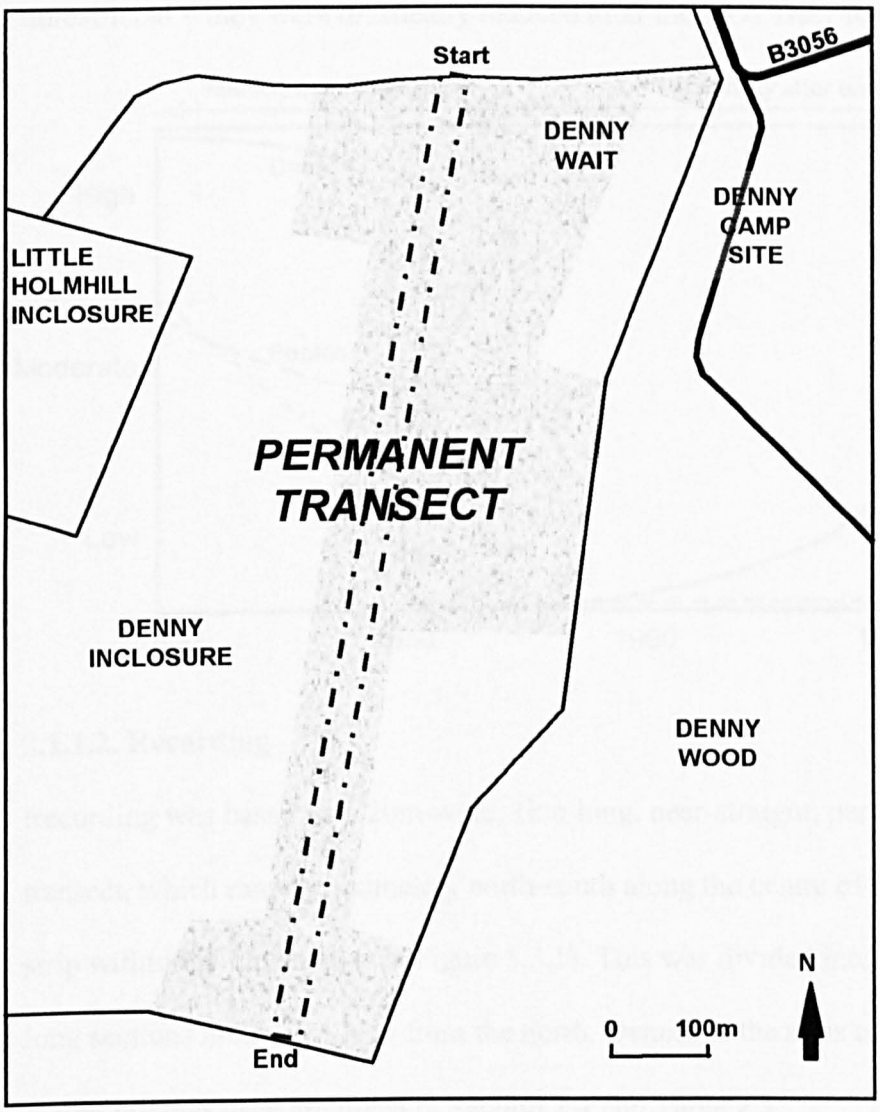
3.1.1.1. Site details

Denny Inclosure is located in the New Forest, south England (see Figure 2.1, Table 2.1). Chadwick (1955), Mountford *et al.* (1999), Peterken *et al.* (1999) and Tubbs (2001) give details of the site and area. It forms part of the 2900ha of 'Ancient and Ornamental', old-growth, beech-oak-holly, woodland found across the New Forest. Most of this has been treated as wood-pasture for centuries and now constitutes one of the finest survivals in Europe of this traditional form of management. Denny was designated as a Forest Nature Reserve as early as 1952 (though much of the original area has been lost), and is now effectively managed as a National Nature Reserve in agreement with English Nature and under the stewardship of the Forestry Commission.

The Inclosure covers about 20ha and is part of a plateau at 30-40m above sea level. It is underlain by a series of stiff, gleyed clays and marls, which are prone to waterlogging in winter and severe drying in summer. The associated soils are moderately acidic stagnogleys. At the extreme northern end, the ground slopes away and is underlain by free-draining, sandy podsolic soil. The area studied was covered mainly by beech and pedunculate oak growing over an understorey of holly (see Appendix for scientific names of species). Minor species included ash, downy and silver birch, sycamore and yew. The ground vegetation was generally sparse, but in places bent-grasses, bracken, purple moor-grass and soft rush were abundant. The vegetation corresponded mostly to communities W14-15 of the National Vegetation Classification (Rodwell 1991) and stand types 8B-D of Peterken (1993a).

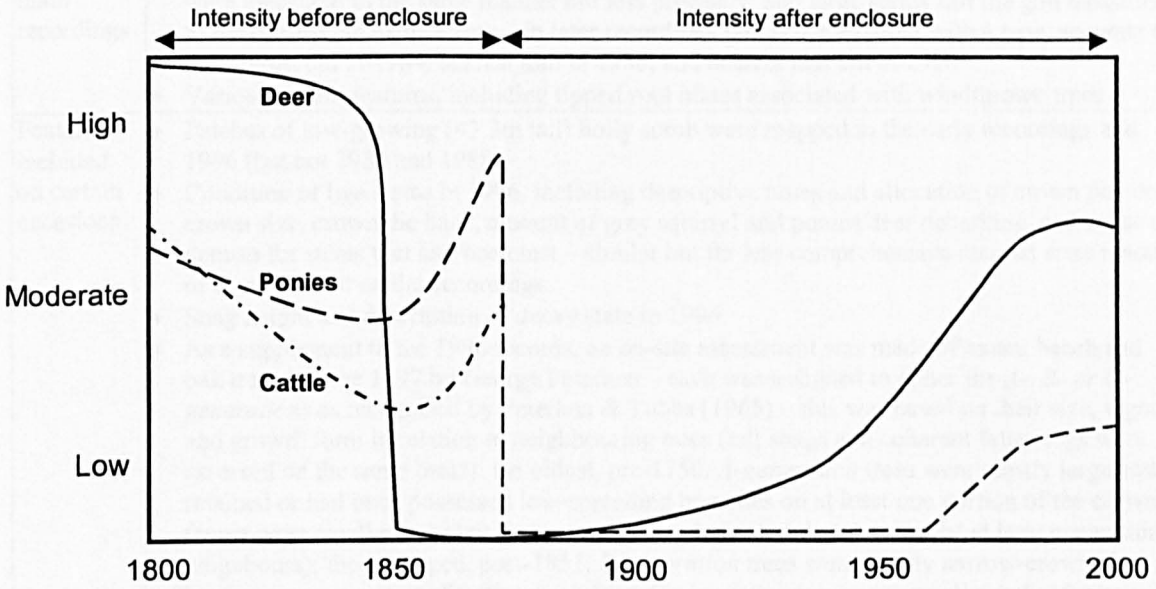
Until 1870 the area was part of Denny Wood and the unenclosed New Forest wood-

Figure 3.1.1: Denny Inclosure site map showing the location of the permanent transect studied, adjoining mature broadleaved stands (shaded), livestock fences (thin lines) and metalled roads (thick lines)



pastures as a whole. At this date part was fenced off to form Denny Inclosure. By 1915 this had been infilled by vigorous natural regeneration. During the 20th century, much of broadleaved area within the Inclosure was felled and replaced with conifer plantations. A 1km-long and 100m-wide strip was, however, protected and left untreated and some other broadleaved blocks were also retained (Figure 3.1.1). Despite remaining fenced, deer and ponies increased in the Inclosure from the 1960s (Figure 3.1.2), as they did across the whole of the New Forest (Tubbs 2001). Notable recent disturbances include the severe drought of 1976 and prolonged dry period thereafter, which resulted in widespread die back of mainly large beech, and also damaging windstorms in 1987 and 1990.

Figure 3.1.2: General changes in the relative intensity of large herbivores in Denny Inclosure from 1800 to 2000 (taken from Figure 2 of Mountford & Peterken 2003). The area was open to ponies and cattle, but in 1870 these were excluded – from around 1960, ponies started to regain access. Deer (mostly fallow deer *Dama dama*) have remained unrestricted – they were drastically reduced after the 1851 Deer Removal Act



3.1.1.2. Recording

Recording was based on a 20m-wide, 1km long, near-straight, permanently marked transect, which ran approximately north-south along the centre of the protected, untreated strip within the Inclosure (see Figure 3.3.1). This was divided into fifty, contiguous, 20m-long sections numbered 1-50 from the north. Details of the aims of recording and methodologies used are given in Section 2.4 and Table 2.3.

Records were made on various occasions from 1954 to 1996, with features recorded at each date being shown in Table 3.1.1. Most records were drawn onto a set of A4 scale charts, each covering a 20m long transect section. Staff and students from Southampton University carried out the recording before 1996 under the supervision of Noel Chadwick, Joyce Lambert, John Manners and Peter Edwards. Nearly all sections were included in the recordings of July 1959 (excluding 26, 44-45), June 1964 (excluding 25-26, 44-45), November 1984 (excluding 26, 44-45), December 1988 (excluding 26, 44-45), and September 1996 (excluding 44-45). Sections 44 and 45 were never recorded because they

Table 3.1.1: Details of the records made on the permanent study transect in Denny Inclosure

Features included at all of the main recordings	• All individuals ≥1.3m height, giving their location, species and status • Gbh or dbh of all stems – in 1956, 1958, 1959 and 1964 small stems were measured using callipers and averaged from the narrowest and widest dbh to the nearest cm; medium stems were measured in the same manner but less precisely; and large stems had the gbh measured to the nearest cm using string – in later recordings gbh was measured with a tape, accurate to the nearest cm in 1984, nearest mm in 1988, and nearest half cm in 1996 • Various salient features, including tipped root plates associated with windthrown trees
Features included on certain occasions	• Patches of low-growing (<1.3m tall) holly scrub were mapped in the early recordings and 1996 (but not 1984 and 1988). • Condition of live stems in 1996, including descriptive notes and allocation of crown position, crown size, crown die back, amount of grey squirrel and ponies/deer debarking, and cause of demise for stems that had been lost – similar but far less comprehensive records were made of some trees at earlier recordings. • Snag height and description of decay state in 1996. • As a supplement to the 1996 records, an on-site assessment was made of extant beech and oak trees in June 1997 by George Peterken – each was assigned to either the *A-, B- or C-generations* as recognised by Peterken & Tubbs (1965) – this was based on their size, vigour and growth form in relation to neighbouring trees (tall snags and coherent fallen logs were assessed on the same basis): the oldest, pre-1750, *A-generation* trees were mostly large and retained or had once possessed low-spreading branches on at least one portion of the crown (some were smaller trees but their crown shape indicated that they predated later generation neighbours); the mid-aged, post-1851, *B-generation* trees were mostly narrow-crowned having grown-up in confined space; whilst *C-generation* trees were smaller individuals adjudged to have developed after 1920. • Fallen dead wood abundance, condition and distribution in 1996 – this was done using twenty-five, 20m long line transects, positioned every 40m across the middle of the transects, and by measuring the diameter or girth (to nearest cm) of all fallen dead stems ≥5cm diameter where they crossed the lines – in addition, all fallen dead logs within the transects that were ≥12.5cm diameter at their mid-point and ≥2m length were mapped – the origin and condition of all recorded pieces was noted – large fallen dead trees were mapped in earlier recordings, but the criteria was not placed on record. • Extent of canopy gaps in: (i) 1954 and 1985 in sections 1-4, 8, 13, 18, 23, 33; and (ii) 1996 in all sections except 44-45, including notes on their origin and understorey infilling. • Extent and composition of ground vegetation in: (i) percentage cover of all vascular species estimated in each section in 1959; (ii) main patches and species mapped in the nine sections (1-4, 8, 13, 18, 23, 33) in 1985; and (iii) main patches and dominant species recorded in all sections in 1996.

had been largely cleared of trees. Partial recordings were carried out in May 1956 (odd numbered sections between 3-33, with some only part-recorded) and in May 1958 (sections 24-40 except 34 and 39, with some only part-recorded). In addition, some supplementary records were made in 1954, 1985, 1989 and 1997.

3.1.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. Firstly, the analysis focused on the general changes in stand composition and structure

since the area was enclosed in 1870 and up to late-1950s, based on an assessment of the 1954-9 records. Stand change thereafter and to 1996 was examined in more detail by comparing the features recorded in 1954-9 with those recorded later.

All transect sections were combined for the analyses, though there was some variation in the distribution of certain species and generations. The area included at each date depended on the number of recorded sections: 0.4086ha were used for 1956; 1.92ha for 1958/9 (NB: the partial recording of 1958 was used not separately as it was done only a year before the near-complete recording of 1959 – however the 1958 data for section 26 was added to the 1959 records, as this section was left out then); 1.84ha from 1964; 1.88ha from 1984 and 1988; and 1.92ha from 1996. Several parameters were expressed per unit area so that changes over each period could be compared, even though the 1956 records were markedly incomplete, so apparent changes to 1959 and later dates might have been biased due to differences in the sampling base.

During the 40 years of observations information on 2421 stems/individuals/seedlings/logs was collected. A small number of mistakes and apparent errors were corrected for and various assumptions were made. The main problems were with: (i) matching up some of the stems/individuals recorded at different dates, including after the hiatus in recoding over 1964-84; and (ii) inaccuracies in the dbh/gbh size measurement of stems, especially in the early records (this appeared to be partly related to changes in the procedure for measuring dbh/gbh and particularly the use of callipers as opposed to tape measures, but also because recorders were careless). Various standard measures were calculated, with annual rates of change being based on 3.3 growing seasons over 1956-59, 4.7 seasons over 1959-64, 20.5 seasons over 1964-84, 4.0 seasons over 1984-88, and 8.0 seasons over 1988-96.

Further to the on-site classification of oak and beech into specific generations it was necessary to do the same for long-dead individuals. This was based on their dbh in 1959 and the dbh range of surviving trees at the same date. Thus, A-generation oak were taken as ≥45cm dbh in 1959; A-generation beech as ≥55cm dbh in 1959; B-generation oak as ≥15 and <45cm dbh in 1959; B-generation beech as ≥10 and <55cm dbh in 1959; C-generation oak as <15cm dbh in 1959; and C-generation beech as <10cm dbh in 1959. While there may be a few misclassifications between the A- and B-generations and the division between B- and C-generations is somewhat arbitrary, the resulting analysis was considered more informative than an analysis based solely on size, because the fate of tree generations is the underlying issue.

Low-growing holly scrub occurred as isolated individuals and as larger patches. Small patches retained their integrity, but some larger patches disintegrated into smaller patches. Change in the total population was determined by regarding each discrete patch as a separate individual.

3.1.2. Results

3.1.2.1. Stand development before 1956-9

The study transect was enclosed from wood-pasture in 1870 and then left to develop without treatment for 85-90 years before the initial recordings of 1956-9. By this time it was covered by high forest with seven tree and shrub species present (Table 3.1.2). Beech and oak dominated the overstorey, whilst holly dominated the understorey, and minor species included ash, birch, sycamore and yew. The basal area was high reflecting the old-growth stature of the stands.

The 1958/9 beech population ranged from saplings to canopy dominants up to 133cm dbh. It included a mixture of A-, B- and C-generation trees (n = 62, 254 and 297 respectively),

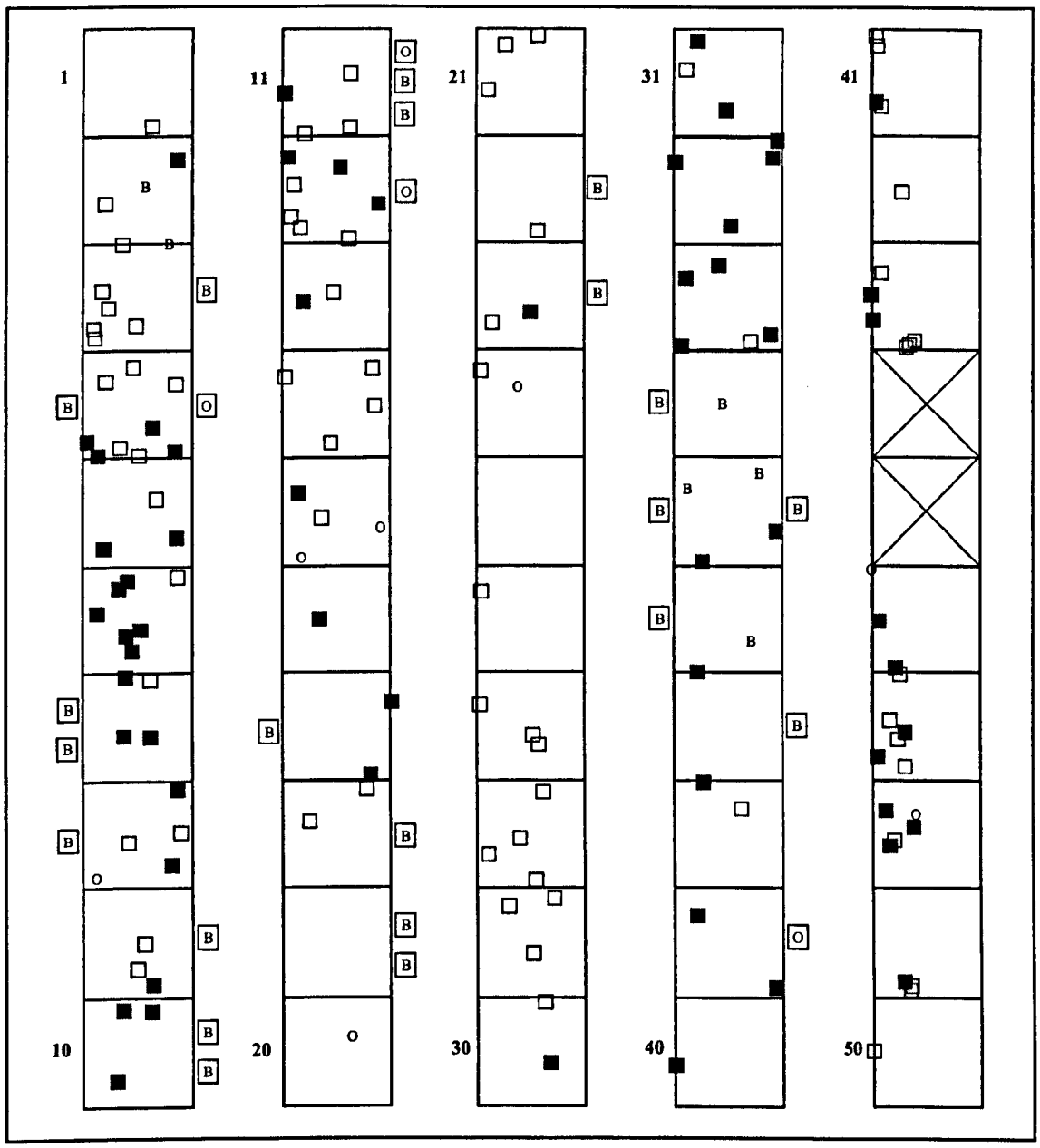
Table 3.1.2: Basal area, density and size-class distribution for live individuals/stems recorded on the permanent transect in Denny Inclosure in 1956 and 1958/9. Includes all individuals ≥1.3m height and all recorded stems

	1956			1958/9			Dbh size-class (cm) 1958/9 (n stems)										
	Basal area (m^2 ha^{-1})	Individuals (n ha^{-1})	Stems (n ha^{-1})	Basal area (m^2 ha^{-1})	Individuals (n ha^{-1})	Stems (n ha^{-1})	<10	10-<20	20-<30	30-<40	40-<50	50-<60	60-<70	70-<80	80-<100	100-<140	All sizes
Beech	26.8	367	367	25.0	319	321	192	180	95	54	28	19	20	10	8	11	617
Oak	21.0	64	64	18.3	73	73	-	8	35	21	13	13	14	17	12	7	140
Holly	1.3	191	201	1.8	285	318	445	155	9	1	-	-	-	-	-	-	610
Birch	0.2	2	2	0.6	4	4	-	-	-	2	5	1	-	-	-	-	8
Ash	<0.1	5	5	<0.1	3	3	-	4	1	-	-	-	-	-	-	-	5
Sycamore	<0.1	17	17	<0.1	14	14	26	-	-	-	-	-	-	-	-	-	26
Yew	<0.1	2	2	<0.1	1	1	1	1	-	-	-	-	-	-	-	-	2
All species	49.4	649	658	45.9	698	733	664	348	140	78	46	33	34	27	20	13	1408

only three of which were multi-stemmed with two-three stems each. The dbh size distribution generally conformed to a negative exponential (Table 3.1.2), indicative of prolonged, steady recruitment continuing to the 1950s. The oak population also included trees up to 122cm dbh. Most were categorised as A- or B-generation trees (n = 70 and 68 respectively), with only two in the C-generation. The dbh size distribution was irregular with few small individuals (Table 3.1.2), indicative of irregular recruitment and a failure of recent regeneration. The holly population included 755 individuals with 609 live stems. The individuals were sub-divided into 534 upright and 14 fallen live individuals ≥1.3m tall/long, plus 207 low-growing bushes. Most individuals were single stemmed, but 10% were multi-stemmed with up to five stems present. The dbh size distribution (Table 3.1.2) suggested that recruitment had been steady for several decades. However, it had possibly declined recently as stems of <5cm were slightly less frequent than stems of 5-<10cm dbh, though the smallest class may have been under-recorded.

Trees present before 1850, as represented by the A-generation, included a sub-equal mixture of oak and beech, which was also indicated by descriptions of the wood in 1565 and 1787 (see Mountford *et al.* 1999). Of those trees that could be assessed from the transect records, 81 were oak and 66 were beech. Pollards were widely scattered, but slightly clustered, occurring in or beside sections 2-23 and 34-39 (Figure 3.1.3). The wood appeared to have been mainly a mosaic of oak- or beech-dominated stands (within which beech was more patchy than oak): in 1958/9 the basal area of remaining A-generation oak and beech in each transect section was negatively correlated, though the relationship was only moderately strong (Table 3.1.3). The largest and apparently oldest trees included both pollard and maiden trees. Crown shape indicated that some pollards had space to expand when they were last cut, but several had narrow crowns indicating that neighbouring trees had confined their development. Whereas maiden oak were a sub-equal mixture of spreading and narrow-crowned trees, maiden beech were mainly narrow-crowned. The

Figure 3.1.3: Position of A-generation beech maidens (■), beech pollards (B), oak maidens (□), and oak pollards (O) in or near the permanent transect in Denny Inclosure in 1958/9. Numbers refer to sections (44 and 45 were not recorded). Pollards growing within 20m of the transect in 1996 are shown beside the transect in boxes



early 18th century stand had thus developed as a widely-spaced scatter of pollard and maiden trees, which had been infilled by narrow-crowned trees, a few of which were pollards. Some areas must have had a closed canopy, but various gaps persisted.

Regeneration between 1850 and the early 20th century was represented by the B-generation (Figure 3.1.4). The great majority was beech, but oak succeeded well on the

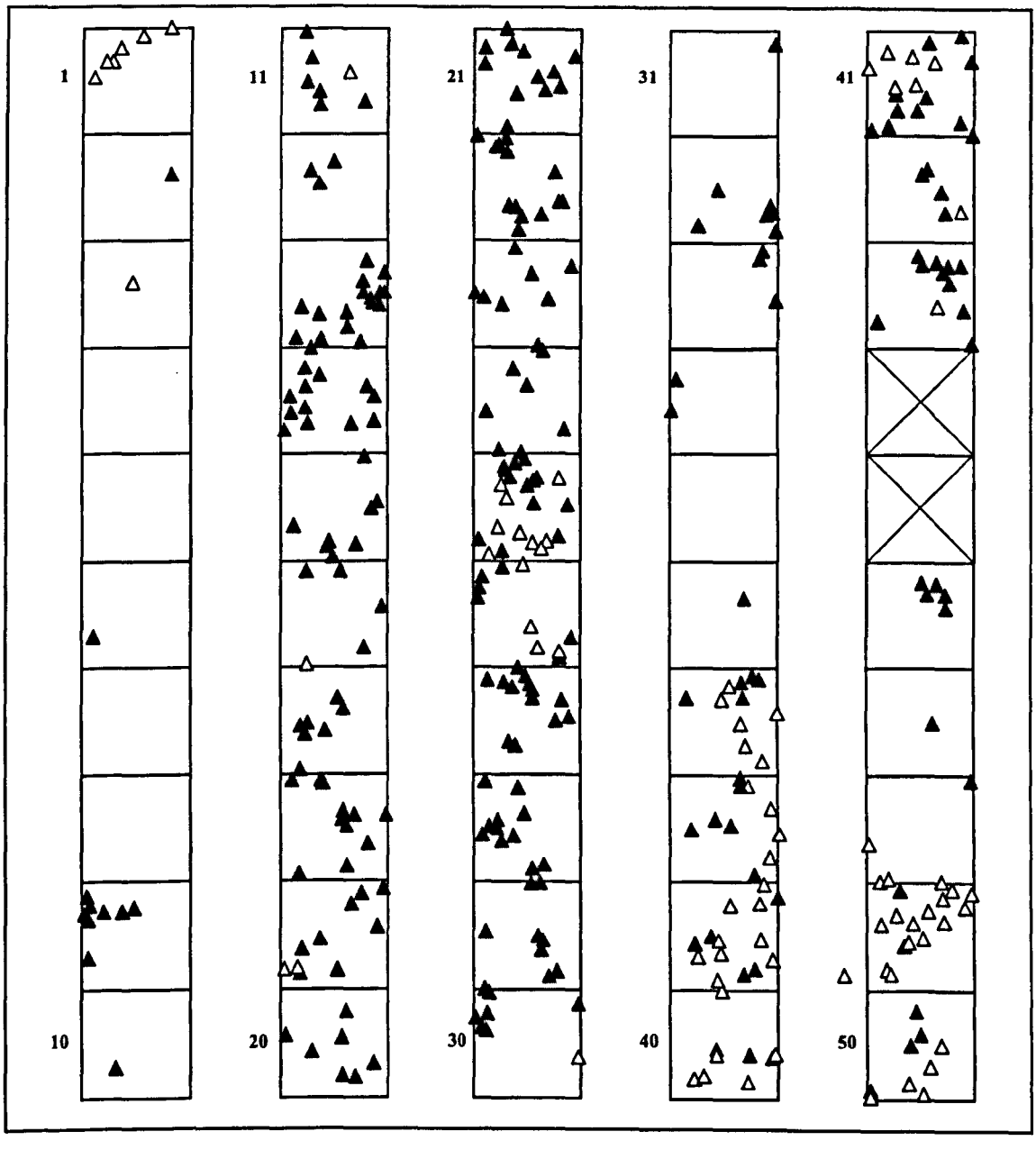
Table 3.1.3: Comparison of the basal area in each section of the permanent transect in Denny Inclosure in 1958/9 for beech, oak, holly and sycamore (A-/B-/C- refer to specific generations), and also for the area covered by holly scrub. The table shows the Spearman rank correlation coefficients (r_s) (lower left half) and significance levels for these (upper right half) (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant). Based on data from 48 sections (each 400m^2). The basal area is based on all live stems ≥1.3m height

Species and generation	Beech A	Beech B	Oak A	Oak B	Beech + oak A	Beech + oak B	Holly	Holly scrub	Beech C	Syca-more C	Oak C
Beech A	-	***	**	**	***	***	ns	ns	**	ns	ns
Beech B	-0.590	-	ns	ns	***	***	ns	ns	**	*	ns
Oak A	-0.303	-0.072	-	*	***	ns	*	ns	**	ns	*
Oak B	-0.290	0.139	-0.272	-	***	***	ns	ns	ns	ns	ns
Beech + oak A	0.595	-0.540	0.488	-0.509	-	***	*	ns	ns	ns	ns
Beech + oak B	-0.620	0.856	-0.129	0.563	-0.663	-	ns	ns	**	*	ns
Holly	-0.119	0.119	0.260	-0.103	0.245	-0.014	-	***	*	*	ns
Holly scrub	0.038	0.030	0.088	0.230	0.142	0.177	0.503	-	**	**	ns
Beech C	-0.396	0.414	0.338	0.043	-0.048	0.432	0.280	0.345	-	**	ns
Sycamore C	0.116	-0.261	0.168	-0.194	0.108	-0.283	-0.246	-0.405	-0.295	-	ns
Oak C	0.072	-0.063	-0.266	0.148	-0.109	0.003	0.093	0.161	-0.017	-0.071	-

northern and southern margins and in localised patches within the body of the wood. In 1958/9, the basal area of remaining B-generation trees in each transect section was strongly negatively rank correlated with that of A-generation beech, but not significantly related to the basal area of A-generation oak, indicating that the B-generation had succeeded in gaps and around oaks (Table 3.1.3). In particular, the strength of the negative correlation between and A- and B-generation beech basal areas suggested that younger beech had been strongly inhibited by the older beech generation. The overall result seems to have been a more or less closed stand along the entire transect by the early 20th century.

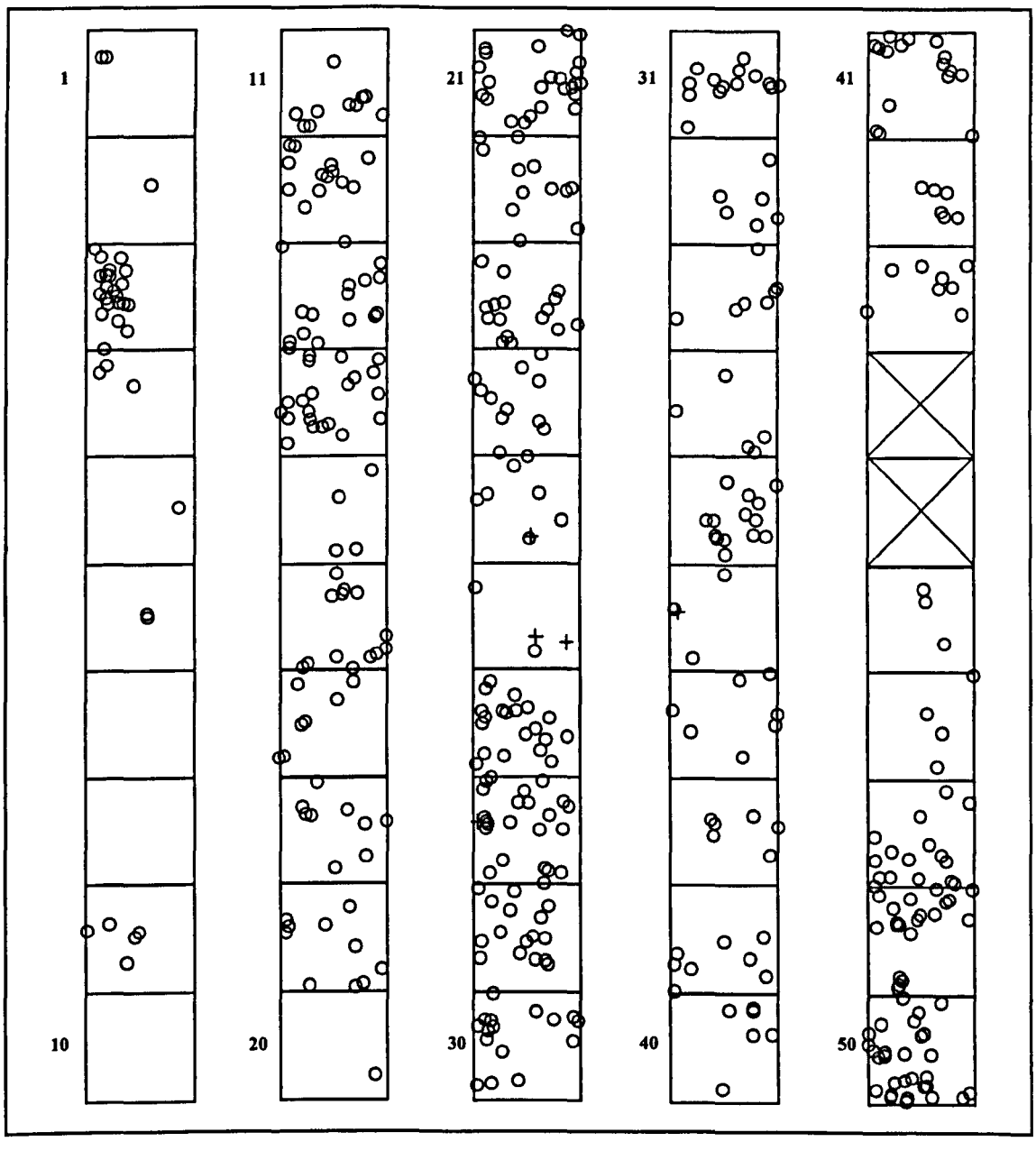
Regeneration between the early 20th century and 1956-9 was represented by the C-generation (Figure 3.1.5). Almost all of these were beech, consistent with stand being more or less closed whilst this generation was establishing. The distribution of survivors in 1958/9 was patchy. The basal area of C-generation beech individuals in each transect section was: (i) negatively rank correlated with A-generation beech; (ii) positively rank correlated with A-generation oak; (iii) positively rank correlated with B-generation beech and B-generation trees as a whole; (iv) positively rank correlated with holly/holly scrub;

Figure 3.1.4: Position of B-generation beech (▲) and oak (△) trees in the permanent transect in Denny Inclosure in 1958/9. Numbers refer to sections (44 and 45 were not recorded)



and (v) weakly negatively rank correlated with C-generation sycamore (Table 3.1.3). This indicated that the beech C-generation was a continuation of the B-generation, having developing particularly in the vicinity of old oaks and holly and mostly away from areas with sycamore regeneration. In fact, the 27 sycamore saplings recorded over 1956-9 were virtually restricted to first few transect sections, and formed part of a recent invasion into the north-east end of the Inclosure mainly below gaps (Chadwick 1955). The basal area of holly in 1958/9 was (weakly) positively rank correlated with oak and all A-generation t

Figure 3.1.5: Position of C-generation beech (O) and oak (+) trees in the permanent transect in Denny Inclosure in 1958/9. Numbers refer to transect sections (44 and 45 were not recorded)



(Table 3.1.3). This indicated it had developed best around old trees and especially oaks. The area covered by low-growing holly was positively rank correlated with the B-generation oak basal area: both were concentrated towards the southern end of the transect.

Only five ash, two yew and seven birch trees, all in the B-generation, were recorded in 1958/9 (Table 3.1.2). The ash and yew ranged from 7-20cm dbh and were found almost entirely in sections 26/27, presumably on more base-rich soils. The birch were larger (35-

53cm dbh) and four were associated with the wood margins at the north end of the transect. Two other birch at 13-20cm dbh formed snags within the wood, having been excluded.

Canopy gaps appeared scarce, but a few were present where four large beech snags of 67-127cm dbh stood (these appeared to have died following a sequence of very wet and very dry summers in the 1950s, personal communication George Peterken). The same was evident from the supplementary records of 1954, other early observations, and the description of the area made by Chadwick (1955). However, the gaps in sections 6-11, which eventually became extensive, were already developing. Similarly, the crown shapes of surviving trees suggested that small gaps had formed occasionally during the first half of the 20th century. Nevertheless, the great majority of snags in 1958/9 (175 out of 203) were <20cm dbh and most A/B-generation snags were amongst the smallest in their group. This indicated that stem exclusion had been the predominant process behind mortality in the preceding decades, with little disturbance-related mortality. Exclusion appeared to have especially affected oak, as it accounted for 17 of the 20 snags sized 30-58cm dbh.

Thus, at the outset of the present study the stand was a mosaic of patches with different initial states and subsequent histories of recruitment. Figures 3.1.3-5 and Table 3.1.4 summarises this in so far as it was sampled by the transect and also taking into account the character of stands nearby, which contained some pollard trees, indicating that the transect crossed only the margins of some well-defined patches. A-generation beech were concentrated in Zones B-C and F, which were also the zones where the nine pollard beech were recorded. B-generation beech were common throughout, save for the zones at start and end of the transect and those already densely stocked with A-generation beech. C-generation beech were sparse in Zones A-B, but common elsewhere, and particularly dense in Zone I. A-generation oaks were prominent in Zones D-E, and scattered thinly through other zones. Most were maiden trees, but a widely scattered seven were pollards. The

Table 3.1.4: General composition and generation structure of zones crossed by the permanent transect in Denny Inclosure. The descriptions are based on the character in 1958/9 and take account of nearby stands

Zone	Sections	A-generation	B-generation	C-generation	Holly
A	1	Few oaks on margin of wood	Several oak and birch	Few beech	Sparse; few new recruits
B	2-8	Dominated by patches of beech or oak; some beech pollards	Few beech, oak and birch	Limited, but dense patch of beech and sycamore	Sparse; medium and small-girth stems
C	9-12	Many beech with some oak; some beech pollards	Some beech and little oak	Some beech and very few sycamore	Moderately dense; few medium and small-girth stems
D	13-17	Scatter of mainly oak with few beech; some pollard and spreading oaks	Many beech with very few oak and birch	Many beech	Fairly sparse; few medium and small-girth stems
E	18-29	Scatter of mainly oak with few beech; few oak pollards; marginal to beech-dominated area with many pollards	Dense beech with one group of oak in formerly sparse area; patch with few ash and yew; very few birch	Dense beech and very few oak in formerly sparse area	Patchy but mostly moderately dense; several large, some medium and many small-girth stems; one very large and several small scrub patches
F	30-36	Many beech with few oak; patch of beech pollards; many spreading beech maidens	Few beech and very few oak	Patchy; some dense beech groups and very few oak	Mostly moderately dense; medium and small-girth stems; several scrub patches
G	37-41	Thin scatter of oak and beech; few pollards	Dense mix of oak and beech; very few birch and yew	Some beech and very few oak	Fairly sparse; few large and some medium/small-girth stems; much scrub
H	42-48	Mix of oak and some beech; many oaks spreading	Patchy; mainly beech with few oak and odd yew	Patchy; beech only	Mostly dense; few large and many medium/small-girth stems; much scrub
I	49-50	Few oaks and very few beech on margin of wood	Dense oak with few beech	Dense beech	Moderately dense; mainly small-girth stems; much scrub

B-generation oaks were concentrated at the start and end of the transect and in parts of Zones E and G. Holly was most abundant in Zones E-F and H, where stems of all sizes occurred together. Patches of low-growing holly scrub were most extensive in the three most southerly zones.

3.1.2.2. General changes from 1956-9 to 1996

3.1.2.2.1. Canopy gaps

Canopy gaps increased substantially and by 1996 covered 29% of the transect. They had an irregular distribution and included some substantial openings, including seven sections with >70% gaps (Figure 3.1.6). Most were connected with beech losses following the 1976 drought or wind damage in storms of the late 1980s/early 1990s. The canopy had already

broken in many of the nine sections recorded in 1985, when sections 8, 13 and 33 contained >40% gaps and sections 1-4 had 10-20% gaps. Small gaps in sections 6-11 were detected as early as 1954.

3.1.2.2.2. Change in the ground vegetation

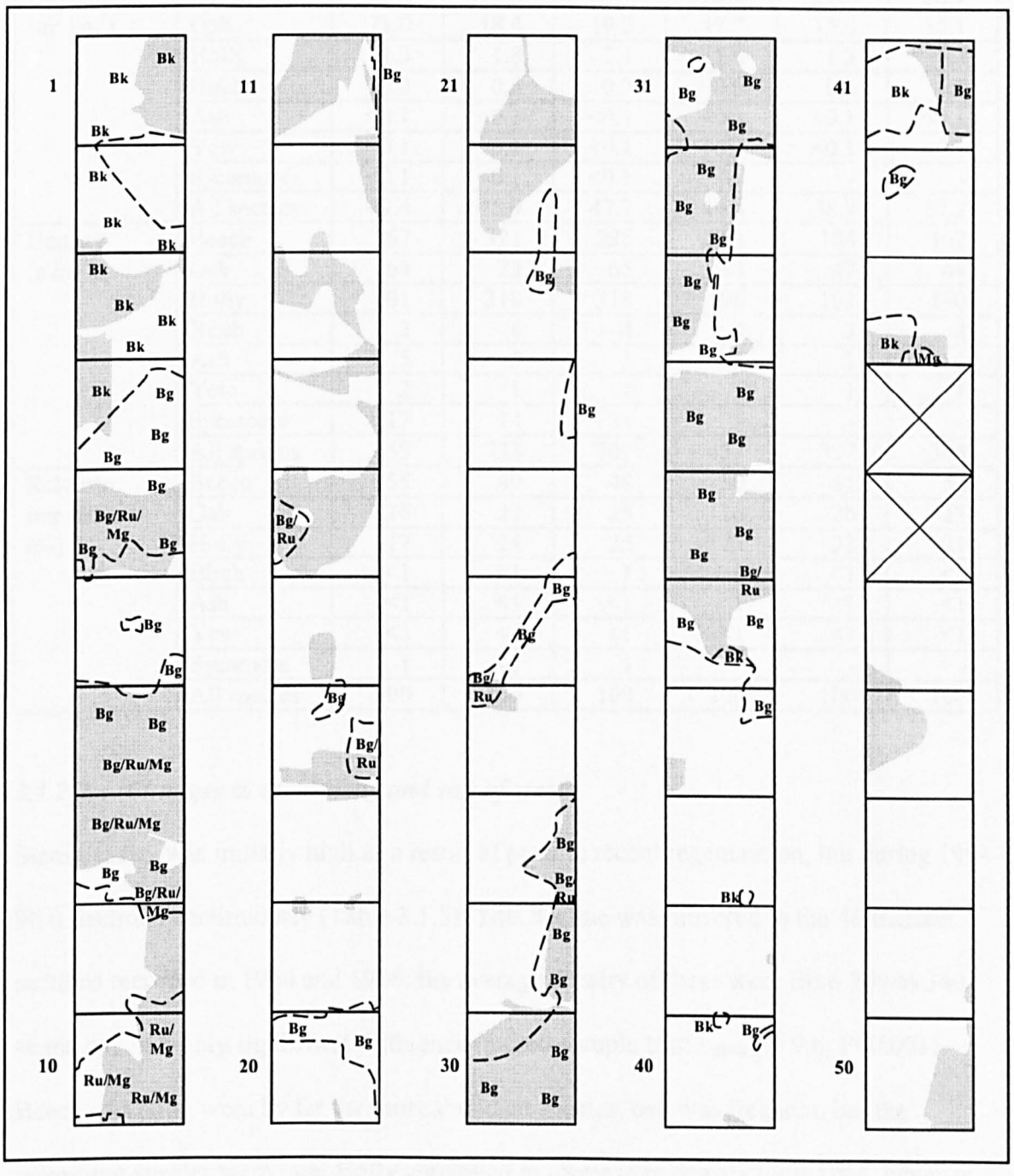
The ground vegetation recorded in 1959 comprised 15 herbaceous, 13 graminoid and five fern species. Most species were scarce. Only bracken and wood sorrel had >5% cover in any one section. Three sections lacked any ground vegetation and cover exceeded 10% in only four sections (sections 1 and 3, mainly bracken; sections 5 and 21, mainly wood sorrel).

By 1996 extensive patches dominated by bracken or grasses had developed, principally below canopy gaps (Figure 3.1.6). The range of species had diminished, especially the herbs and ferns, but purple moor-grass and soft rush were prominent in wet areas, and foxglove was frequently associated with decaying beech logs. A few patches of butcher's broom remained in sections 23/24, but these were hard-grazed. Similar patches of bramble grew on and around windthrown trees in sections 4, 29 and 40. These changes were already well advanced in the nine sections recorded in 1985.

3.1.2.2.3. Changes in stem basal area

The stand basal area was particularly high in 1956, related to the sampling bias at this recording. It remained high to 1964, but declined continuously thereafter (Table 3.1.5). This decline was mirrored in the 46 transect sections recorded in 1964 and 1996: the average basal area of these went from 47.7 to 36.5m^2 ha^{-1}, a highly significant difference (paired-sample test: $t_{(df=45)} = 5.1$, $P<0.001$). There was a steep drop in basal area during 1984-88, due to losses from the October 1987 storm and delayed mortality of beech

Figure 3.1.6: Location of canopy gaps (shaded) and extent of ground vegetation (dashed lines) along the permanent transect in Denny Inclosure in 1996. Dominant ground vegetation species are distinguished: Bg = bent-grasses, Ru = soft rush, Mg = purple moor-grass, Bk = bracken. Numbers refer to transect sections (sections 44 and 45 were not recorded)



following the 1976 drought. Beech and oak together made up 94-96% of the total basal area at all recordings. All the main species declined in basal area, but the fall over 1964-96 was only 20-21% for beech and oak, whereas holly declined by 42% and birch by 75%.

Table 3.1.5: Change in the basal area, density and relative importance of live stems recorded on the permanent transect in Denny Inclosure from 1956 to 1996. Includes all recorded stems ≥1.3m height. Relative importance = [% total basal area + % all stems]÷2

		1956	1958/9	1964	1984	1988	1996
Basal area (m^2 ha^{-1})	Beech	26.8	25.0	25.7	24.4	21.6	20.7
	Oak	21.0	18.4	19.2	17.7	15.6	15.1
	Holly	1.3	1.8	2.1	1.6	1.3	1.2
	Birch	0.2	0.6	0.7	0.6	0.4	0.2
	Ash	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
	Yew	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
	Sycamore	<0.1	<0.1	<0.1	-	-	-
	All species	49.4	45.9	47.7	44.4	38.9	37.2
Density (n ha^{-1})	Beech	367	321	298	202	184	162
	Oak	64	73	65	54	47	44
	Holly	201	318	318	196	162	130
	Birch	2	4	4	4	3	2
	Ash	5	3	1	1	1	1
	Yew	2	1	1	1	1	1
	Sycamore	17	14	21	-	-	-
	All species	658	733	709	457	397	340
Relative importance (%)	Beech	55	49	48	50	51	52
	Oak	26	25	25	26	26	27
	Holly	17	24	25	23	22	21
	Birch	<1	<1	1	1	<1	<1
	Ash	<1	<1	<1	<1	<1	<1
	Yew	<1	<1	<1	<1	<1	<1
	Sycamore	1	<1	1	-	-	-
	All species	100	100	100	100	100	100

3.1.2.2.4. Changes in the density and size of stems

Stem density was initially high as a result of prolific recent regeneration, but during 1964-96 it declined continuously (Table 3.1.5). This decline was mirrored in the 46 transect sections recorded in 1964 and 1996: the average density of these went from 709 to 340 stems ha^{-1}, a highly significant difference (paired-sample test: $t_{(df=45)} = 9.6$, $P<0.001$). Beech and holly were by far the most abundant species, oak was frequent, but the remaining species were rare. Holly continued to increase in density until 1964, whereas beech and oak declined slightly. Thereafter, all of these declined but with holly decreasing most (by 59% of its 1958/9 level), followed by beech and then oak (by 50% and 40% respectively). This made a major contribution to the overall decline in the relative importance of holly. Apparent changes over 1956-58/9 for the less numerous species were due primarily to the sampling bias in 1956. Even so, sycamore continued to increase until

1964. However, by 1984 all sycamores had died, though the species persisted as tall poles nearby. Ash almost died out, but two yews, the other species associated with more fertile soils, persisted. Although birch declined overall, during 1988-96 two birch managed to recruit on top of a tipped beech root plate.

The size-class distribution of all stems combined changed over 1959-96, though it remained negatively exponential (Figure 3.1.7). Initial densities in the smallest (0-<20cm dbh) and medium (60-<80cm dbh) classes were relatively high, reflecting the recent wave of understorey regeneration and combined effect of fast-grown B-generation and slow-grown A-generation trees. Although the density of trees between 30-90cm dbh remained virtually unchanged, larger trees declined moderately, whilst smaller trees declined greatly.

3.1.2.3. Changes in the beech population from 1956-9 to 1996

3.1.2.3.1. Survival, mortality and recruitment patterns

804 individual beech stems were recorded within the transect (another 19 recorded were just outside). At the first full transect recording in 1959, 617 beech were alive and 106 formed snags (in addition, another ten live beech were recorded in section 26 in 1958, but these were not recorded again until 1996). The live trees in 1959 included 62 A-generation, 248 B-generation and 297 C-generation. These fell to 311 live trees by 1996 (Table 3.1.6): 309 were survivors from the 1959 population, whilst the other two were secondary stems on existing individuals that appeared to have grown above 1.3m height after 1959 (possibly they were simply overlooked in the 1959/64 recordings).

After 1959, mortality rates varied substantially between generations and periods (Table 3.1.6). The rates were inversely related to age between 1959 and 1984: this was apparent in both the rates for each generation and the general decrease in mortality rate for C-generation as it aged. However, mortality of the older generations accelerated after 1984,

Figure 3.1.7: Change in the dbh size-class distribution of live stems recorded on the permanent transect in Denny Inclosure from 1959 to 1996. Includes all recorded stems ≥1.3m height

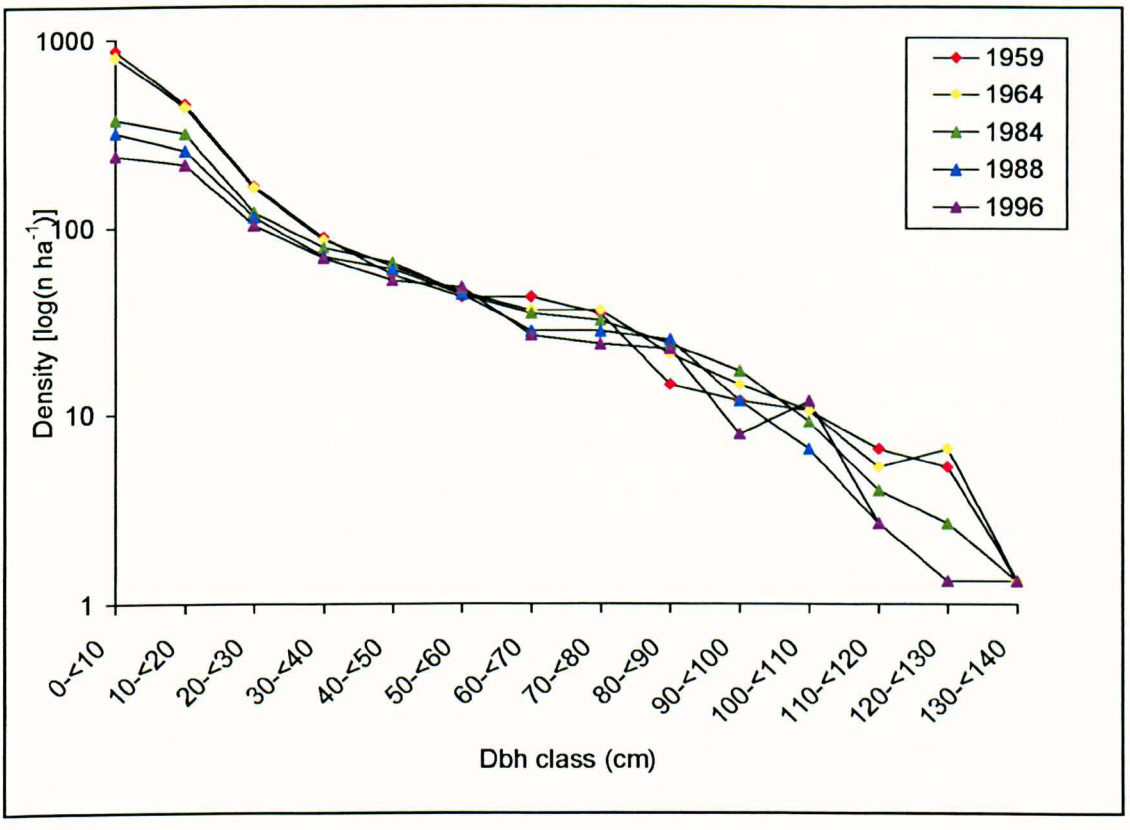


Table 3.1.6: Change in the number of live beech stems of each generation in the permanent transect in Denny Inclosure for four periods between 1959 and 1996. Based on changes in 46 transect sections*

Total population (n)	A-gen	B-gen	A+B-gen	C-gen	
1959	62	248	310	297	
1964	59	234	293	270	
1984	49	185	234	146	
1988	42	173	215	131	
1996	34	152	186	116	
Losses and recruits (n)	A-gen	B-gen	A+B-gen	C-gen	C-gen
1959-64	-3	-14	-17	-58	+31
1964-84	-10	-49	-59	-127	+3
1984-88	-7	-12	-19	-15	0
1988-96	-8	-21	-29	-15	0
Mortality rate (m % a^{-1})	A-gen	B-gen	A+B-gen	C-gen	
1959-64	1.05	1.23	1.19	4.52	
1964-84	0.90	1.14	1.09	3.05	
1984-88	3.78	1.66	2.09	2.67	
1988-96	2.61	1.60	1.79	1.51	

* section 24-25 was omitted in 1964 so it was assumed that one B-generation and two C-generation trees in this section, which were alive in 1959 and dead by 1984, were still alive in 1964

particularly in the A-generation. The rates for 1984-88 were generally higher than the trends, due mainly to delayed mortality from the 1976 drought (the October 1987 windstorm blew down and killed one A- and two B-generation beech, whilst six A- and three B-generation trees >40cm dbh died and remained as snags in 1988 probably because they died due to drought effects). Mortality in both the A- and B-generations was noticeably episodic. Many large trees died in the 1976 drought or in later years from its effects (Table 3.1.7), and the lesser droughts of the 1980s and 1990s appear to have hastened the death of already weakened trees. Several were uprooted or snapped by wind (Table 3.1.8), including seven prostrate windthrown trees that remained alive in 1996 despite being uprooted during storms. Windthrow occurred in all periods, but was most frequent during 1988-96, indicating that the storms of 1990 had the most impact. Windthrow created new gaps, but often it enlarged existing ones. Some large falling trees evidently brought down or crushed others.

Table 3.1.7: Survival and mortality in relation to size for beech stems in the permanent transect in Denny Inclosure between 1959 and 1996. Size-classes are based on initial dbh in each period. The table shows the number of stems in each category. Based on data from 46 transect sections*

		1959-64		1964-84		1984-88		1988-96	
	Dbh (cm)	Survived	Died	Survived	Died	Survived	Died	Survived	Died
A-gen	25<40	2	-	2	-	1	-	-	1
	40-<60	15	1	12	1	10	-	8	2
	60-<80	24	1	20	2	18	1	13	3
	80-<100	7	1	8	3	9	4	11	-
	100-<140	11	-	7	4	4	2	2	2
B-gen	15-<20	65	8	37	17	15	3	8	3
	20-<30	85	5	67	22	66	1	57	9
	30-<40	51	1	45	5	40	5	36	5
	40-<50	20	-	20	4	22	2	24	2
	50-<60	8	-	9	1	21	1	18	2
	60-<80	5	-	7	-	9	-	9	-
C-gen	<10	152	40	79	94	50	6	34	6
	10-<15	87	18	52	28	48	3	47	6
	15-<20	-	-	12	4	29	4	32	2
	20-<30	-	-	-	-	4	2	3	1

* section 24-25 was omitted in 1964 so: (i) it was assumed that one B-generation and two C-generation trees in this section, which were alive in 1959 and dead by 1984, were still alive in 1964; and (ii) the size of stems as measured in 1959 was used for surviving stems

Table 3.1.8: Number of beech trees that were thrown over/broken by the wind or died standing in the permanent transect in Denny Inclosure between 1959 and 1996. The table shows the number of stems in each category. The footnotes explain about trees that were crushed or probably killed by squirrel debarking. Based on changes in 46 transect sections

		Wind damaged		Died standing	
		Wind-thrown[a]	Wind-snapped	Recorded as snag[b]	Potentially died as snag[c]
A+B-gen	Before 1959	-	-	19	0
	1959-64	3	3	12	1
	1964-84	6[d]	-	28	23
	1984-88	7	1	13	3
	1988-96	14	1	12	4
C-gen	Before 1959	-	-	23	37
	1959-64	3[e]	-	31	27
	1964-84	-	-	8	116[f]
	1984-88	1	-	3[g]	12
	1988-96	-	-	9[h]	6[g]

[a] = includes fallen trees that remained alive on the ground for several years before dying; [b] = certainly died standing; [c] = small dbh stems that potentially died standing, but had collapsed within the period; [d] = includes four small stems crushed by large windblown oak; [e] = all crushed by windblown oak; [f] = includes one stem not recorded in 1964 and assumed to have survived; [g] = both include one stem probably killed by squirrel debarking; [h] = all probably killed by squirrel debarking

Mortality was also patchy, with several groups of trees being killed by drought and/or wind damage. Mortality of A-generation trees was concentrated in Zone B in 1964-84, Zone F in 1984-88, and in both of these zones in 1988-96. B-generation mortality was clustered in Zone D in 1964-84 and E in 1984-96. Over 1959-96, mortality of both generations combined was high in Zones D and F (56-64%), moderate in Zones B-C, E and G (27-44%) and low in Zones H-I (17%-none). Even in zones where mortality was higher, there were places where all or most A- and B-generation beech survived.

C-generation beech were abundant in 1959, but only 38% of the 1959 population survived to 1996 (Table 3.1.6). Survival rates varied considerably at the scale of sections and smaller, i.e. survival was much better in some groups than in others. Almost all died standing (Table 3.1.7). During the 1980s debarking by grey squirrels became increasingly severe, and the incidence of debarking by deer and ponies also increased. Recruitment virtually ceased after 1964 (Table 3.1.6). The 31 recruits between 1959 and 1964 were

concentrated in the first six sections – 20 were in section 3 – where canopy gaps had already developed. All were dead by 1984. The three recruits between 1964 and 1984 were sprouts from the base of older individuals: two survived to 1996, but the other individual, which had been growing quite rapidly, was dead standing by 1988, having been ring-barked by grey squirrels.

Mortality within each period of observation varied by size (Table 3.1.8) and in relation to previous dbh increment rates. In the A-generation, mortality during the main periods of drought (1964-88) was associated with trees >80cm dbh (based on combined size-classes in Table 3.1.8; $\chi^2_{1964\text{-}84(df=1)} = 5.5$, $P<0.05$; $\chi^2_{1984\text{-}88(df=1)} = 7.6$, $P<0.01$): the drought-induced losses included four slow-growing (dbh increment of zero cm a^{-1} or less in period before death), one medium-growing (0.22cm dbh a^{-1} during 1964-84), and five fast-growing victims (four fastest during 1959-64 and third fastest during 1984-88). A-generation losses due to windthrow/snap included stems of all sizes, and four of the seven that died after 1988 had been growing at least moderately well until 1988 (0.10-0.34cm dbh a^{-1}).
In the B-generation, competition between individuals appeared to be the principal cause of death, especially before the stands were opened by the 1976 drought and later storms: none of the largest stems died, mortality during 1959-64 and 1964-84 was significantly associated with smaller stems sized <30cm dbh (based on combined size-classes in Table 3.1.8; $\chi^2_{1959\text{-}64(df=1)} = 7.4$, $\chi^2_{1964\text{-}84(df=1)} = 8.9$, both $P<0.01$), and 18 of the 39 losses during 1964-84 had been very slow-growing (dbh increment of zero or less in 1959-64). Even so, several fast-growing B-generation stems also succumbed before the 1976 drought, including 12 in 1964-84 that were amongst the 15 fastest growing in 1959-64. This contrasts with 1984-1996, when mortality of fast-growing B-generation trees was invariably due to windthrow/snap and not to exclusion processes. This suggests that fast-growing individuals may have been vulnerable killed to bark-stripping by grey squirrels in

1964-1984, when most would have been within the vulnerable 10-40cm dbh size range (Section 3.1.2.3.3.2).

Whilst the canopy remained largely closed the C-generation remained in the understorey and competition between individuals appears to have been a major cause of death: this was especially evident in 1964-84 when mortality was associated with the smallest <10cm dbh size-class (based on combined size-classes in Table 3.1.8; $\chi^2_{(df=1)} = 10.8$, $P<0.01$) and 25 of the 83 stems that died had been very slow-growing (dbh increment of zero cm a^{-1} or less in 1959-64). However, other causes of mortality were evident. Mortality was never confined to the smallest size-class (Table 3.1.8), and in 1964-84 and 1984-88 death overtook 46 of the 47 and 5 of the 15 respectively of the hitherto fastest-growing stems. The most likely causes were increased bark-stripping by grey squirrels (from the 1970s) and increased browsing by deer and ponies (from the 1960s). Squirrels certainly killed 7 of the 9 fastest-growing C-generation trees that died during 1988-96 and left many of 10-40cm dbh survivors badly debarked (see Table 3.1.13).

3.1.2.3.2. Growth of beech

Dbh and basal area increments varied greatly between individual beech trees. The regression of dbh increment on initial size was significant over the whole of 1959-96, but accounted for only 8% of the variation (Table 3.1.9). There was a slight tendency for larger individuals to have grown faster than smaller, particularly in the B- and C-generations (Figure 3.1.8). The fastest increments were recorded for a minority of medium-large trees in 1959. Very large A-generation and many other trees in the B- and C-generations grew slowly. Where the A- and B-generation initial size-range overlapped (40-70cm dbh), the most vigorous members of the later generation were growing larger than the least vigorous members of the preceding generation. These trends were apparent in the average rank of the dbh increment rates for each generation over 1959-96: this was similar

Table 3.1.9: Results of the stem increment analysis for beech in the permanent transect in Denny Inclosure. The table shows the regressions comparing dbh increment (inc_{dbh}, cm a^{-1}) against initial dbh (ini_{dbh}, cm) and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2) during 1959-96. Lognormal data were transformed before analysis. Figures 3.1.8-3.1.10 show the relationships as scatter plots

(a) Dbh increment v initial dbh

Period	Dbh increment	n	F	P	r^2%
1959-96	$\log(inc_{dbh+1}) = 0.0359.\log(ini_{dbh+1}) + 0.0372$	279	23.6	<0.001	7.9
1959-64	$\log(inc_{dbh+1}) = 0.1306.\log(ini_{dbh+1})^2 - 0.2202.\log(ini_{dbh+1}) + 0.1460$	453	29.1	<0.001	11.1
1964-84	$\log(inc_{dbh+1}) = 0.0254.\log(ini_{dbh+1}) + 0.0338$	298	5.3	=0.02	1.8
1984-88	$inc_{dbh} = -0.4740.\log(ini_{dbh+1})^2 + 1.2580.\log(ini_{dbh+1}) - 0.6104$	286	6.6	=0.002	4.4
1988-96	$inc_{dbh} = -0.4133.\log(ini_{dbh+1})^2 + 1.1340.\log(ini_{dbh+1}) - 0.4458$	282	8.5	<0.001	5.7

(b) Basal area increment v initial basal area

Period	Basal area increment	n	F	P	r^2%
1959-96	$\log(inc_{ba+1}) = 0.4338.\log(ini_{ba+1}) - 0.01359$	278	419.9	<0.001	60.3
1959-64	$\log(inc_{ba+1}) = 0.1667.\log(ini_{ba+1})^2 - 0.1894.\log(ini_{ba+1}) + 0.2851$	397	179.0	<0.001	47.6
1964-84	$\log(inc_{ba+1}) = 0.1179.\log(ini_{ba+1})^2 - 0.0675.\log(ini_{ba+1}) + 0.1905$	278	114.5	<0.001	45.4
1984-88	$\log(inc_{ba+1}) = -0.1408.\log(ini_{ba+1})^2 + 1.1575.\log(ini_{ba+1}) - 1.1243$	235	46.3	<0.001	28.5
1988-96	$\log(inc_{ba+1}) = -0.0926.\log(ini_{ba+1})^2 + 0.8914.\log(ini_{ba+1}) - 0.6211$	278	117.1	<0.001	46.0

(c) Basal area increment v initial basal area (excluding all negative and zero increments)

Period	Basal area increment	n	F	P	r^2%
1959-96	as above	278	419.9	<0.001	60.3
1959-64	$\log(inc_{ba+1}) = 0.1086.\log(ini_{ba+1})^2 + 0.0866.\log(ini_{ba+1}) + 0.2138$	305	615.8	<0.001	80.3
1964-84	$\log(inc_{ba+1}) = 0.0985.\log(ini_{ba+1})^2 + 0.0093.\log(ini_{ba+1}) + 0.1892$	259	159.7	<0.001	55.5
1984-88	$\log(inc_{ba+1}) = 0.4896.\log(ini_{ba+1}) - 0.3165$	220	220.4	<0.001	50.3
1988-96	$\log(inc_{ba+1}) = -0.0908.\log(ini_{ba+1})^2 + 0.8773.\log(ini_{ba+1}) - 0.5852$	275	134.0	<0.001	49.6

for A- and B-generation trees, but lower for the C-generation (Table 3.1.10a/b). Some of the variation in the increment rates was related to stratification: trees that ended up in the canopy or sub-canopy with medium or larger crowns generally grew faster than those with smaller crowns in the sub-canopy or trees in the understorey (Table 3.1.11).

Increment in basal area over 1959-96 was more strongly related to initial size, with the linear regression accounting for 60% of the total variation (Table 3.1.9). There was a strong tendency for larger individuals to have grown faster than smaller, especially in the B- and C-generations (Figure 3.1.8). The highest rates were achieved by a small number of larger-sized, A- and B-generation trees in 1959. The slowest grown trees were mainly small, C-generation individuals. This was reflected in the average rank of the basal area increment rates for each generation: this was highest for the A-generation, less for B-generation, and least for the C-generation (Table 3.1.10a/b). The increment rates were

Figure 3.1.8: Relationship between (above) the dbh increment and initial dbh and (below) the basal area increment and initial basal area of beech stems in the permanent transect in Denny Inclosure over 1959-96. Parameters for the regression lines shown are given in Table 3.1.9. Some symbols represent more than one stem

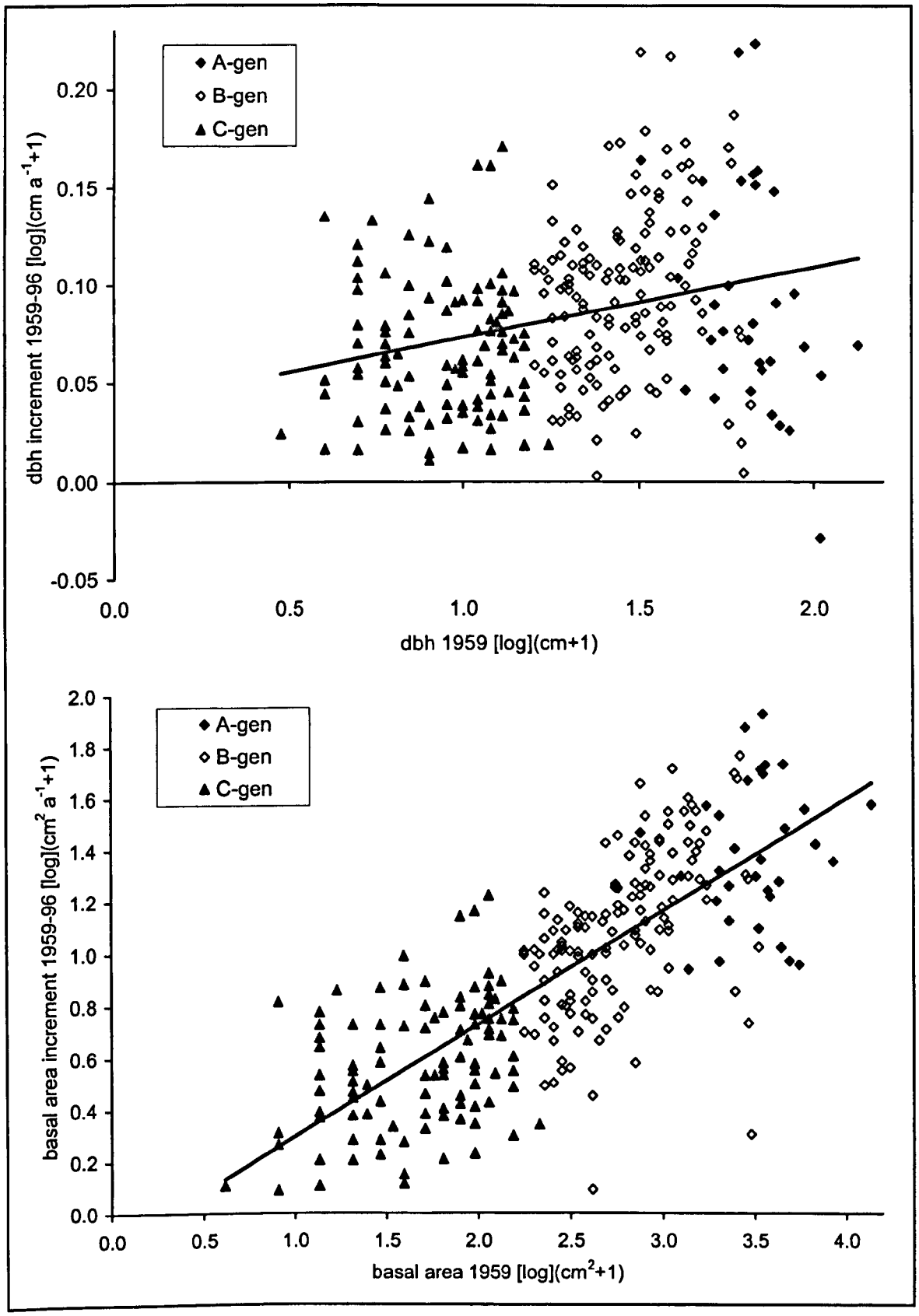


Table 3.1.10: Comparison of the stem increment rates for each generation of beech in the permanent transect in Denny Inclosure during 1959-96. The tables show: (a) the median rate and average rank based on changes in stem dbh (cm a^{-1}) and basal area (cm^2 a^{-1}); (b/c) the significance of the differences between the average ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests; and (d) the Spearman rank correlation coefficients (r_s) comparing the increment rates in successive periods for stems that survived throughout and were reliably measured at each recording (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant)

(a) Median and average ranks

Period		Dbh increment			Basal area increment		
		A-gen	B-gen	C-gen	A-gen	B-gen	C-gen
1959-96	*stem number*	*33*	*139*	*107*	*33*	*139*	*107*
	median	0.191	0.245	0.157	21.9	11.3	2.6
	average rank	148.3	162.0	108.8	222.8	174.6	69.5
1959-64	*stem number*	*45*	*196*	*212*	*45*	*196*	*212*
	median	0.638	0.213	0.213	87.9	8.6	1.8
	average rank within 1959-64	336.0	227.6	203.3	358.8	248.1	179.5
	average rank between periods	116.0	308.4	257.9	325.7	289.6	225.7
1964-84	*stem number*	*40*	*144*	*114*	*40*	*144*	*114*
	median	0.165	0.193	0.112	16.6	7.9	1.8
	average rank within 1964-84	150.5	167.5	126.4	187.5	178.7	99.3
	average rank between periods	72.5	286.2	211.8	190.1	290.6	225.7
1984-88	*stem number*	*41*	*142*	*103*	*41*	*142*	*103*
	median	0.000	0.207	0.175	0.0	10.5	3.1
	average rank within 1984-88	102.3	150.3	150.5	131.5	162.3	122.4
	average rank between periods	52.5	279.0	267.9	167.9	284.1	290.5
1988-96	*stem number*	*33*	*141*	*108*	*33*	*141*	*108*
	median	0.187	0.291	0.310	22.6	15.8	5.6
	average rank within 1988-96	91.8	151.0	144.3	174.5	177.0	85.0
	average rank between periods	74.2	376.6	352.2	271.5	393.1	379.1

(b) Comparison of average ranks for A-, B- and C-generation beech within each period

Dbh increments

	$H_{(df=2)}$	P	significant pair-wise comparisons
1959-96	26.7	<0.001	A>C (Q=2.46)*; B>C (Q=5.13)***
1959-64	39.0	<0.001	A>B (Q=5.07)***; A>C (Q=6.24)***
1964-84	14.4	=0.001	B>C (Q=3.80)***
1984-88	11.9	=0.003	A<B (Q=3.28)**; A<C (Q=3.16)**
1988-96	14.3	=0.001	A<B (Q=3.28)**; A<C (Q=3.16)**

Basal area increments

	$H_{(df=2)}$	P	significant pair-wise comparisons
1959-96	142.1	<0.001	A>B (Q=3.09)**; A>C (Q=9.54)***; B>C (Q=10.13)***
1959-64	79.1	<0.001	A>B (Q=5.13)***; A>C (Q=8.37)***; B>C (Q=5.31)***
1964-84	63.1	<0.001	A>C (Q=5.57)***; B>C (Q=7.35)***
1984-88	14.9	=0.001	B>C (Q=3.73)**
1988-96	84.0	<0.001	A>C (Q=5.52)***; B>C (Q=8.82)***

(c) Comparison of average ranks for A-, B- and C-generation beech between each period

Dbh increments

	$H_{(df=3)}$	P	significant pair-wise comparisons
A-gen	43.7	<0.001	59-64>[64-84/84-88/88-96] (Q≥4.35)***
B-gen	26.0	<0.001	88-96>[59-64/64-84/84-88] (Q≥4.30)***
C-gen	47.7	<0.001	88-96>[59-64/64-84/84-88](Q≥4.95)***; 64-84>[59-64/84-88] (Q≥2.64)*

Basal area increments

	$H_{(df=3)}$	P	significant pair-wise comparisons
A-gen	63.2	<0.001	59-64>88-96 (Q≥2.79)*, [64-84/84-88] (Q≥5.71)***; 88-96>[64-84/ 84-88] (Q≥4.66)***
B-gen	37.1	<0.001	88-96>[59-64/64-84/84-88] (Q≥5.85)***
C-gen	81.8	<0.001	88-96>[59-64/64-84/84-88] (Q≥5.24)***; [59-64/84-88]>64-84 (Q≥3.11)*

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Table 3.1.10: continued

(d) Correlation between increment rates for individual stems in successive periods

Periods	Rates compared	A-generation (27 stems)		B-generation (103 stems)		C-generation (81 stems)	
		r_s	P	r_s	P	r_s	P
1959-64 v	Dbh increment	-0.276	<0.001	-0.093	ns	-0.025	ns
1964-84	Basal area increment	-0.283	<0.001	0.073	ns	0.119	ns
1964-84 v	Dbh increment	0.368	<0.001	0.165	<0.01	0.472	<0.001
1984-88	Basal area increment	0.355	<0.001	0.192	<0.01	0.541	<0.001
1984-88 v	Dbh increment	0.519	<0.001	0.401	<0.001	0.362	<0.001
1988-96	Basal area increment	0.505	<0.001	0.393	<0.001	0.535	<0.001

Table 3.1.11: Comparison of the increment rates over 1959-96 for beech stems in various crown position/size categories in 1996 in the permanent transect in Denny Inclosure. The table shows: (i) the median rate and average rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the average ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Dbh increment rates ($H_{(df=8)}$ = 44.4, P<0.001)

	n	median	average rank	pair-wise comparison of ranks
(a) Canopy with medium crown	33	0.290	180.8	=bcdf; >g (Q=3.41)*; >ehi (Q≥3.72)**
(b) Canopy with large/very large crown	25	0.271	183.6	=acdf; >eg (Q=3.34)*; >ghi (Q≥3.72)**
(c) Sub-canopy medium/large crown	10	0.241	161.3	=abdefghi
(d) Canopy with small crown	52	0.220	161.9	=abcefg; >hi (Q≥3.20)*
(e) Sub-canopy small crown	66	0.170	117.7	<ab; =cdfghi
(f) Canopy with very small crown	18	0.157	138.3	<a; =bcdeghi
(g) Sub-canopy very small crown	21	0.156	104.9	<ab; =cdefhi
(h) Understorey medium/large crown	30	0.131	103.5	<abd; =cefgi
(i) Understorey very small/small crown	20	0.125	89.5	<abd; =cefgh

(b) Basal area increment rates ($H_{(df=8)}$ = 165.9, P<0.001)

	n	median	average rank	pair-wise comparison of ranks
(a) Canopy with large/very large crown	25	26.0	231.2	=bcde; >fghi (Q≥6.41)***
(b) Canopy with medium crown	33	19.2	213.3	=acde; >fghi (Q≥6.00)***
(c) Canopy with small crown	52	12.3	182.8	=abde; >fghi (Q≥4.99)***
(d) Canopy with very small crown	18	11.6	178.9	=abce; >fg (Q≥3.87)**; >hi (Q≥4.67)***
(e) Sub-canopy medium/large crown	10	9.1	147.4	=abdefghi
(f) Sub-canopy small crown	66	4.5	96.9	<abcd; =fghi
(g) Sub-canopy very small crown	21	3.8	80.1	<abcd; =efhi
(i) Understorey very small/small crown	20	2.1	58.3	<abcd; =efgh
(h) Understorey medium/large crown	30	1.8	56.2	<abcd; =efgi

related to the stratification of trees, with those that ended up in the canopy generally having higher rates than those that ended up in the sub-canopy or understorey (Table 3.1.11).

Increment dbh growth varied in the four periods during 1959-96. The regressions of dbh increment on initial dbh were significant for each period, but again accounted for little of

the total variation (Table 3.1.9). Although the trends were weak, larger-sized trees tended to increase most in the two periods before 1984, but declined in the two periods afterwards (Figure 3.1.9). This was clearly reflected in the average rank of the dbh increment rates for each generation over the four study periods (Table 3.1.10a-c). For the A-generation the average rank was: (i) highest during 1959-64 and significantly higher than the other two generations during 1959-64; and (ii) similar to the other two generations during 1964-84, but significantly lower than them throughout 1984-88-96. For the B-generation the average rank was similar throughout 1959-64-84-88, but higher during 1988-96. For the C-generation the average rank was least during 1964-84 and highest during 1988-96. The B- and C-generations had similar average ranks except during 1964-88, when the B-generation exceeded the C-generation.

The rank dbh increment rates for individual trees were significantly correlated in most periods (Table 3.1.10d). For the A-generation they were: (i) negatively correlated during 1959-64 v 1964-1984, with many trees slowing in growth and especially the fastest growing during 1959-64; and (ii) positively correlated during 1964-84 v 1984-88 and 1984-88 v 1988-96, with many trees maintaining their relative rate of growth. For the B- and C-generations they were: (i) not correlated during 1959-64 v 1964-1984; (ii) strongly positively correlated for the C-generation during 1964-84 v 1984-88 (but only weakly so for the B-generation); and (iii) strongly positively correlated during 1984-88 v 1988-96.

Basal area increments were strongly related to the initial basal area of stems in all four periods during 1959-96 with the regressions between these variables being highly significant. They accounted for 28-48% of the total variation and this increased to 50-80% if all stems with negative or zero increments were excluded (Table 3.1.9). Plots of the regressions showed that in all periods there was a strong tendency for the larger trees to have increased most and the smallest trees least in basal area (Figure 3.1.10).

Figure 3.1.9: Relationships between the dbh increment and initial dbh for beech stems in the permanent transect in Denny Inclosure over (top left) 1959-64, (top right) 1964-84, (bottom left) 1984-88, and (bottom right) 1988-96. Parameters for the regression lines shown are given in Table 3.1.9. Some symbols represent more than one stem

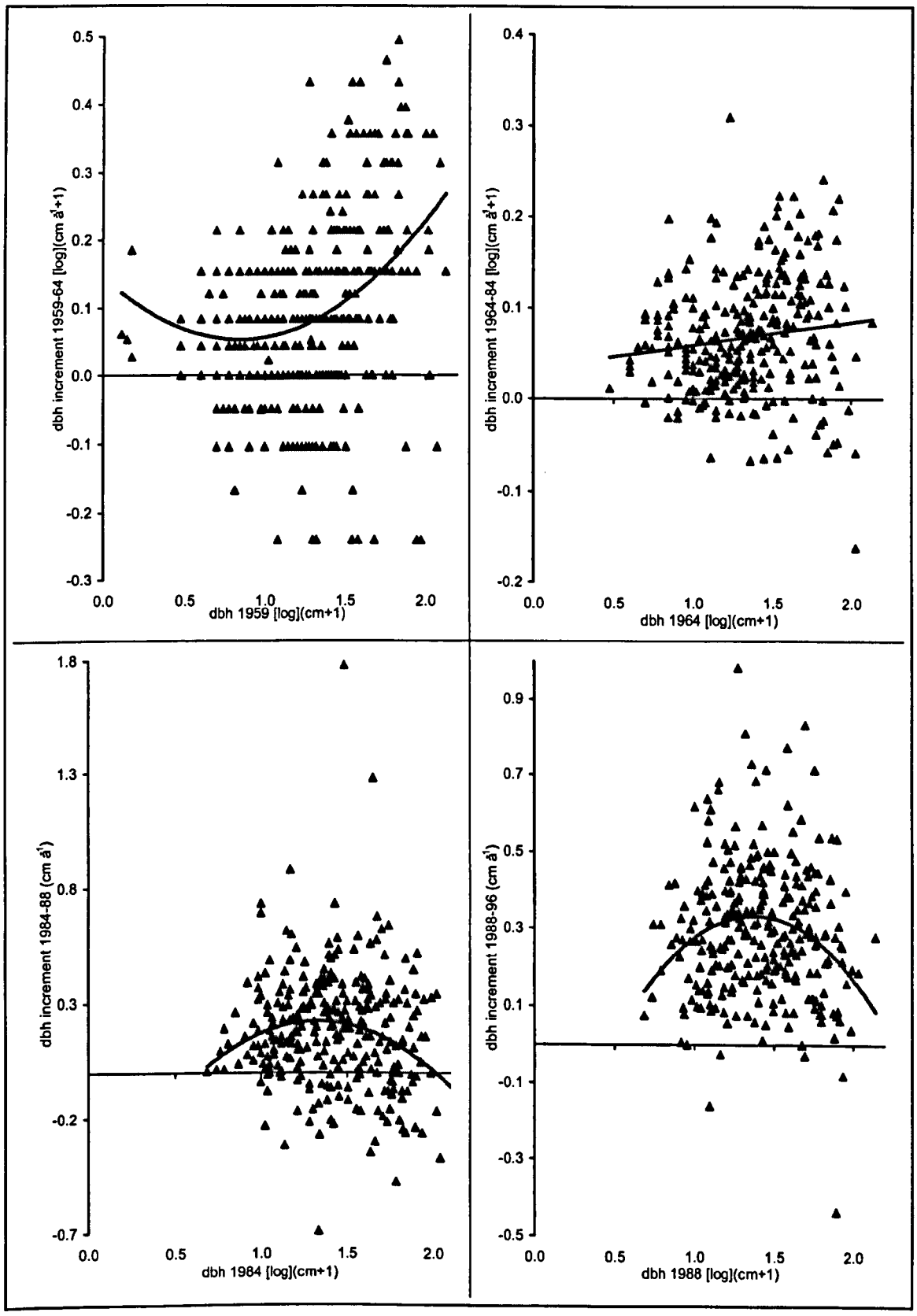
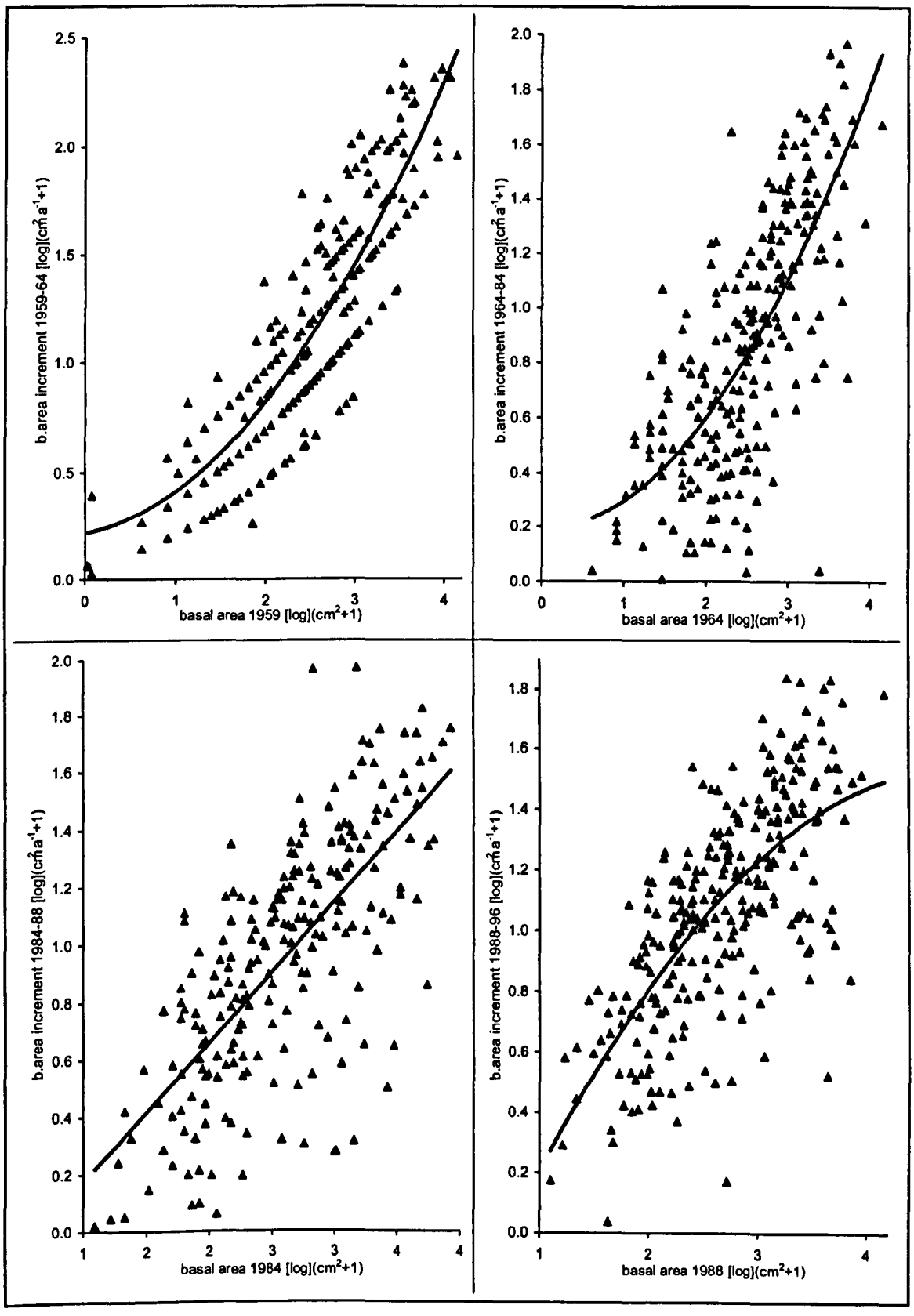


Figure 3.1.10: Relationships between the basal area increment and initial basal area for beech stems in the permanent transect in Denny Inclosure over (top left) 1959-64, (top right) 1964-84, (bottom left) 1984-88, and (bottom right) 1988-96. Stems with negative or zero increments were excluded. Parameters for the regression lines shown are given in Table 3.1.9. Some symbols represent more than one stem



The average rank of the basal area increment rates for each generation differed significantly over the four study periods (Table 3.1.10a-c). For the A-generation this was highest during 1959-64 and higher during 1988-96 than throughout 1964-84-88. For the B-generation it was lower throughout 1959-64-84-88 than 1988-96. For the C-generation it was least throughout 1959-64-84, higher during 1984-88, and highest during 1988-96. During 1959-64 the average rank was highest for the A-generation and least for the C-generation. During 1964-84 and 1988-96 there was no differences between A- and B-generation average ranks, but both exceeded the C-generation. During 1984-88 the B-generation had the highest average: it was significantly higher than the C-generation and almost significantly higher than the A-generation. The rank correlations between the basal area increment rates of individual trees were very similar to those based on the dbh increment rates (see above) (Table 3.1.10d).

3.1.2.3.3. Condition of beech in 1996

3.1.2.3.3.1. Stratification, crown size and crown die back

All live beech trees were given a crown position, size and die back category in 1996 (Table 3.1.12). 141 were placed in the canopy, of which 64 had medium or larger crowns, 108 were put in the sub-canopy and 62 in the understorey. Beech therefore exceeded oak in all layers and especially the lowest two.

Severe or very severe die back was recorded on 77 beech trees, including almost half of those in the understorey (Table 3.1.12). The principle causes were: (i) squirrel debarking – this affected 50 trees, mainly in the sub-canopy and understorey, and in many cases had killed the top or lead to it being snapped out; (ii) drought – this affected the crowns of 17 trees in the canopy and probably went back to the severe drought of 1976 and prolonged dry period thereafter – in several cases associated strips/patches of trunk bark necrosis were observed – some of these and others, with lesser overall die back that also appeared

Table 3.1.12: Stratification and crown condition of live beech trees in the permanent transect in Denny Inclosure in 1996. The table shows the number of stems in each category, including all uprooted trees and the principal cause of deterioration for stems with severe or very severe die back (dr = drought; sq = squirrel debarking; wd = wind breakage; hit = struck by uprooted/wind-snapped tree; up = uprooted; ? = unsure)

Crown layer	Crown Size	Crown die back				Total
		None/part	Moderate	Severe	Very severe	
Canopy	Very large	-	1	1 1dr	-	2
	Large	16	6	1 1dr	-	23
	Medium	26	9	4 3dr, 1dr/sq	-	39
	Small	34	12	5 4dr, 1sq	6 4dr, 1dr/sq, 1sq	57
	Very small	12	2	2 1dr, 1sq	4 1dr, 3sq	20
Sub-canopy	Large	2	-	-	-	2
	Medium	6	2	-	1 1sq	9
	Small	51	10	8 6sq, 1sq/wd, 1hit	5 4sq, 1sp/wd	74
	Very small	11	1	2 2sq	9 5sq, 2hit, 1wd?, 1?	23
Under-storey	Large	2	2 2up	2 2up	1 1sq	7
	Medium	15	5 1up	4 3sq, 1hit	7 7sq	31
	Small	8	-	4 2sq, 1hit/up, 1wd	8 7sq, 1up	20
	Very small	-	1	-	3 2sq, 1hit	4
All	All	183	51	33	44	311

to have suffered from drought die back, were re-shooting strongly and showed clear signs of crown recovery; and (iii) wind damage (including uprooting, trunk/bough breakage, and strikes from other wind-damaged trees) – this affected 12 (or possibly 13) trees in the sub-canopy and understorey – again, some of these and others were re-shooting after having parts or the crown blown out – also, several of the uprooted trees remained in reasonable condition (apart from the crown damage caused during their fall) and had some vigorous new shoots forming off trunk and branches (though often these had been part-debarked by squirrels).

3.1.2.3.3.2. Squirrel debarking

Grey squirrels had debarked two-thirds of the surviving beech in 1996 (Table 3.1.13). The amount and concentration of bark removed varied. In several of the worst cases, much of the bark had been removed from the base or upper part of the main trunk (or even both) over a metre or a few metres length. In other cases it comprised many or several, small-medium patches spread through the tree and often at the very base where the roots joined the main trunk. Some patches appeared to have been stripped long ago but some were

Table 3.1.13: Grey squirrel debarking to standing live beech stems in the permanent transect in Denny Inclosure in 1996. The relationship between stem size and the degree of debarking is shown, with the number of stems given for each category

Dbh (cm)	Maximum debarking category				
	None	Limited	Moderate	Severe	Very severe
<10	12	1	4	1	5
10-<20	17	13	9	22*	19*
20-<30	13	20	8	6*	17*
30-<40	12	13	3	5*	7*
40-<50	12	18	-	-	-
50-<60	11	13	1	1	1
60-<140	25	13	-	-	-
Totals	102	91	25	35	49

* combining stem numbers in each size-class, severe/very severe damage was found to be strongly associated with stems of 10-<40cm dbh ($\chi^2_{(df=1)} = 48.0$, $P<0.001$)

recent. Often stems appeared to have been repeatedly debarked around the same place. Damage was particularly severe to stems of 10-<40cm dbh and especially those that were growing rapidly (Tables 3.1.13-3.1.14). 19% of B-generation trees were severely debarked or ring-barked, but damage was particularly concentrated on the more vigorous C-generation poles with 47% of these in this condition. Although some crown branches on A-generation trees had been debarked or even killed by grey squirrels, overall this never amounted to more than limited debarking on the tree.

Table 3.1.14: Relationship between dbh increment rate and grey squirrel debarking to B- and C-generation beech stems in the most vulnerable size-range (10-<40cm dbh) in the permanent transect in Denny Inclosure in 1996. Stem numbers are shown for three increment rate classes (during 1988-96) and two categories of squirrel damage. Only stems that remained alive, upright and with reliable dbh measurements were included

Dbh increment rate 1988-96 ($cm\ a^{-1}$)	B+C-generations		B-generation		C-generation	
	None, limited or moderate debarking	Severe or very severe debarking	None, limited or moderate debarking	Severe or very severe debarking	None, limited or moderate debarking	Severe or very severe debarking
<0.2	39	9	22	4	17	5
0.2-0.4	48	32	27	9	21	23
>0.4	16	32*	11	13*	5	19*
Totals	103	73	60	26	43	47*

* for each and both generations combined, severe/very severe debarking was associated with the fastest grown stems ($\chi^2_{(df=1)} = 9.04\text{-}17.3$, $P_{min}<0.01$); between the two generations, severe/very severe debarking was associated moreover with the C-generation ($\chi^2_{(df=1)} = 8.8$, $P<0.01$)

3.1.2.4. Changes in the oak population from 1956-9 to 1996

3.1.2.4.1. Survival, mortality and recruitment patterns

107 individual oak stems were recorded within the transect (another four were recorded just outside). At the first full transect recording in 1959, 135 oak were alive and 27 formed snags (in addition, another five live and two snag oak were recorded in section 26 in 1958, but these were not recorded again until 1996). The live trees in 1959 comprised 69 A-generation, 64 B-generation and only two C-generation individuals. By 1996, 53 had died and none recruited, so the population had declined to 82 live trees (Table 3.1.15).

Table 3.1.15: Change in the number of live oak stems of each generation in the permanent transect in Denny Inclosure for four periods between 1959 and 1996. Based on changes in 46 transect sections*

Total population (n)	A-gen	B-gen	A+B-gen	C-gen
1959	69	64	133	2
1964	67	58	125	2
1984	56	45	101	-
1988	48	41	89	-
1996	43	39	82	-
Losses and recruits (n)	A-gen	B-gen	A+B-gen	C-gen
1959-64	-2	-6	-8	0
1964-84	-11	-13	-24	-2
1984-88	-8	-4	-12	-
1988-96	-5	-2	-7	-
Mortality rate (m % a^{-1})	A-gen	B-gen	A+B-gen	C-gen
1959-64	0.62	2.07	1.31	0.00
1964-84	0.87	1.23	1.03	all lost
1984-88	3.78	2.30	3.11	-
1988-96	1.37	0.62	1.02	-

* section 24-25 was omitted in 1964 so it was assumed that two B-generation trees in this section, which were alive in 1959 and dead by 1984, were still alive in 1964

After 1959, mortality rates for all oak trees remained around 1% a^{-1}, except during 1984-88 when the rate trebled (Table 3.1.15). Rates were higher for the B-generation before 1984 and for the A-generation afterwards. Mortality in the A-generation included many trees in the smaller size-classes, which appeared to have been excluded primarily by beech. However, several larger trees died and over the whole span from 1959-96 there no significant association between size and mortality (Table 3.1.16). Some of the large and

Table 3.1.16: Survival and mortality in relation to size for oak stems in the permanent transect in Denny Inclosure between 1959 and 1996. Size-classes are based on initial dbh in each period. The table shows the number of stems in each category. Based on data from 46 transect sections*

		1959-64		1964-84		1984-88		1988-96	
	Dbh (cm)	Survived	Died	Survived	Died	Survived	Died	Survived	Died
A-gen	40-<60	18	2	13	5	7	2	6	1
	60-<80	31	-	24	3	19	3	16	3
	80-<100	12	-	14	2	16	2	16	1
	100-<130	7	-	6	1	5	1	5	-
B-gen	15<30	29	6	12	13	10	2	11	-
	30-<40	16	-	17	-	16	2	13	2
	40-<60	6	-	11	-	15	-	15	-
C-gen	10-<15	2	-	-	2	-	-	-	-

* section 24-25 was omitted in 1964 so: (i) it was assumed that two B-generation trees in this section, which were alive in 1959 and dead by 1984, were still alive in 1964; and (ii) the size of stems as measured in 1959 was used for surviving stems

medium-sized trees were toppled during windstorms (sometimes brought down with toppled neighbouring beech): these were spread through all the periods but with most coming down in the 1990 storms (Table 3.1.17). Other large trees, which died standing, appeared to be laggards that died due to drought effects, but many years after the severe drought of 1976 and because of the prolonged dry period through the 1980s and early 1990s. In contrast, mortality in the B-generation was strongly concentrated in the smallest size classes and all trees appeared to have died standing (Table 3.1.6-3.1.7). Both C-generation trees were lost during 1964-84, having probably been excluded.

Table 3.1.17: Number of oak trees that were thrown over/broken by the wind or died standing in the permanent transect in Denny Inclosure between 1959 and 1996. The table shows the number of stems in each category. Based on changes in 46 transect sections

		Windthrown[a]	Died standing	
			Recorded as snag[b]	Potentially died as snag[c]
A+B-gen	Before 1959	-	26	-
	1959-64	1	7	1
	1964-84	2	8	13
	1984-88	1	10	1
	1988-96	4	3	-
C-gen	Before 1959	-	4	-
	1959-64	-	-	-
	1964-84	-	1	1

[a] = includes fallen trees that remained alive on the ground for several years before dying – all were in A-generation trees; [b] = certainly died standing

Oak mortality was not closely related to vigour, but more hitherto slow-growing trees died. All the eight windthrown trees that died were A-generation individuals: of these four had been very slow growing in the period before death (zero cm dbh a^{-1} or less), but the others had been growing at above median rates. All three large (>75cm dbh) A-generation oaks that died standing after 1984 and were accurately measured had been growing far slower than most other large oaks. Of the 15 B-generation trees that died standing, 11 had been growing well below the median rate, implicating exclusion as a major cause of death. However, four had been growing faster and one that died during 1964-84 grew faster than all the other the B-generation trees during 1959-64.

3.1.2.4.2. Growth of oak

Dbh and basal area increment rates varied greatly between individual oak trees. Over 1959-96, there was no significant regression between the dbh increment and initial dbh (Table 3.1.18). The fastest rates (>0.4cm a^{-1}) were recorded for six A-generation trees of 59-85cm in 1959 and two B-generation trees of 37-39cm dbh (Figure 3.1.11). All very large A-generation and many other trees in both generations grew slowly. However, most medium-large B-generation trees grew at least moderately. Where the size-ranges overlapped (40-50cm dbh in 1959), trees in the B-generation trees grew faster than in the A-generation. Nevertheless, there was no significant difference between the rank dbh increment rates over 1959-96 for the two generations (Table 3.1.19a). Rather, the average rank was higher for trees that ended up in the canopy in 1996 rather than in the sub-canopy or understorey (Table 3.1.20a).

Increment in basal area over 1959-96 was more strongly related to initial size: the linear regression accounted for 37% of the total variation (Table 3.1.18) and showed there was a strong tendency for larger individuals to have grown faster than smaller in both generations (Figure 3.1.11). The fastest rates were recorded in a group of A-generation trees sized 59-

Table 3.1.18: Results of the stem increment analysis for oak in the permanent transect in Denny Inclosure. The table shows the regressions comparing dbh increment (inc_{dbh}, cm a^{-1}) against initial dbh (ini_{dbh}, cm) and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2) during 1959-96. Lognormal data were transformed before analysis. Figures 3.1.11-3.1.13 show the relationships as scatter plots

(a) Dbh increment v initial dbh - no significant regression for any period

(b) Basal area increment v initial basal area

Period	Basal area increment	n	F	P	r^2%
1959-96	$\log(inc_{ba+1}) = 0.6172.\log(ini_{ba+1}) - 0.8185$	63	35.3	<0.001	36.6
1959-64	$\log(inc_{ba+1}) = -0.5679.\log(ini_{ba+1})^2 + 4.0242.\log(ini_{ba+1}) - 5.5193$	72	5.3	=0.007	13.3
1964-84	$\log(inc_{ba+1}) = 0.8338.\log(ini_{ba+1}) - 1.7812$	55	16.9	<0.001	24.2
1984-88	$\log(inc_{ba+1}) = 0.8084.\log(ini_{ba+1}) - 1.5384$	54	17.5	<0.001	25.2
1988-96	$\log(inc_{ba+1}) = 0.5486.\log(ini_{ba+1}) - 0.5974$	73	20.8	<0.001	22.7

(c) Basal area increment v initial basal area (excluding all negative and zero increments)

Period	Basal area increment	n	F	P	r^2%
1959-96	as above	63	35.3	<0.001	36.6
1959-64	$\log(inc_{ba+1}) = 0.5624.\log(ini_{ba+1}) - 0.1677$	62	63.9	<0.001	51.6
1964-84	$\log(inc_{ba+1}) = 0.7850.\log(ini_{ba+1}) - 1.4448$	48	42.0	<0.001	47.7
1984-88	$\log(inc_{ba+1}) = 0.9071.\log(ini_{ba+1}) - 1.7507$	50	43.1	<0.001	47.3
1988-96	$\log(inc_{ba+1}) = -0.4784.\log(ini_{ba+1})^2 + 3.7103.\log(ini_{ba+1}) - 5.7121$	71	13.9	<0.001	29.0

92cm dbh in 1959. The slowest grown were B-generation trees. This was apparent in the comparison of rank basal area increment rates over 1959-96, with the A-generation median being significantly higher than the B-generation (Table 3.1.19a). The increments over 1959-96 were related to the stratification of trees in 1996: those in the canopy at this date had a higher average rank than those in the sub-canopy or understorey (Table 3.1.20a).

Dbh increments varied in the four periods over 1959-96. Nonetheless, the regression of dbh increment on initial dbh was never significant (Table 3.1.18). During 1959-64 many grew relatively rapidly, but throughout 1964-84-88 many trees grew little or declined slightly in size between recordings (Figure 3.1.12). The rates over 1988-96 indicated a general recovery in growth. This was reflected in the rank of the dbh increment rates for the A- and B-generations (Table 3.1.19a/b). There was no significant difference between the median rates for each generation in any of the four periods; but the average rank for the A-generation was significantly higher during 1959-64 than throughout 1964-84-88-96 (with a non-significant in 1988-96); and the average rank for the B-generation was significantly higher during 1959-64 than throughout 1964-84-88, and returned to a

Figure 3.1.11: Relationship between (above) the dbh increment and initial dbh and (below) the basal area increment and initial basal area of oak stems in the permanent transect in Denny Inclosure over 1959-96. Parameters for the regression lines shown are given in Table 3.1.18. Some symbols represent more than one stem

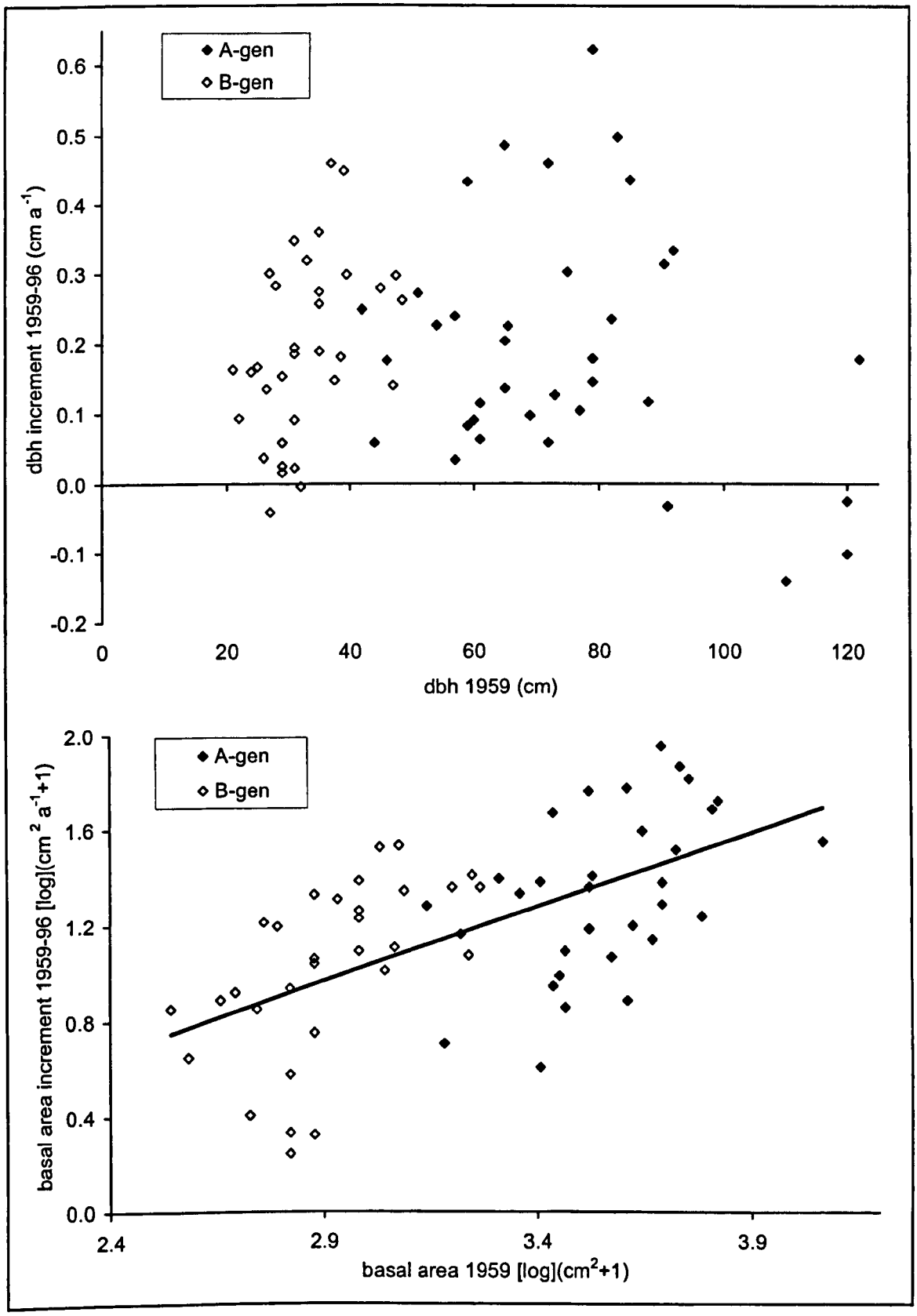


Table 3.1.19: Comparison of the stem increment rates for the oak A- and B- generations in the permanent transect in Denny Inclosure during 1959-96. The tables show the median rate and average rank based on changes in stem dbh (cm a^{-1}) and basal area (cm^2 a^{-1}) and comparisons of: (a) the median for each generation within each period based on a Mann-Whitney two-sample rank (U) test; (b) the average rank based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple (Q) tests; and (c) the individual increment rates in successive periods for stems that survived throughout and were reliably measured at each recording based on Spearman rank correlation (r_s) tests (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant)

(a) Comparison of A- v B-generation within each period

		Dbh increment			Basal area increment		
Period		A-gen	B-gen	comparison	A-gen	B-gen	Comparison
1959-96	*stem number*	*36*	*33*	$U=1240^{ns}$	*36*	*33*	U=1451*
	median	0.176	0.180		18.3	10.5	
1959-64	*stem number*	*45*	*37*	$U=1821^{ns}$	*45*	*37*	U=2093*
	median	0.426	0.426		41.4	19.4	
1964-84	*stem number*	*44*	*30*	$U=1687^{ns}$	*44*	*30*	$U=1746^{ns}$
	median	0.147	0.038		11.0	1.9	
1984-88	*stem number*	*45*	*37*	$U=1756^{ns}$	*45*	*37*	$U=1809^{ns}$
	median	0.000	0.111		0.0	4.4	
1988-96	*stem number*	*40*	*39*	$U=1443^{ns}$	*40*	*39*	$U=1763^{ns}$
	median	0.191	0.275		24.3	14.9	

(b) Comparison of A- v B-generation between each period

			1959-64	1964-84	1984-88	1988-96	H	P	significant pair-wise comparisons
Dbh increments	A-gen	*stem number*	*45*	*44*	*45*	*40*	18.7	<0.001	59-64>[64-84/84-88] (Q≥3.70)**
		median	0.426	0.147	0.000	0.191			
		average rank	111.1	74.5	70.5	94.2			
	B-gen	*stem number*	*37*	*30*	*37*	*39*	28.1	<0.001	[59-64/88-96]>[64-84/84-88] (Q≥3.02)***
		median	0.426	0.038	0.111	0.275			
		average rank	95.1	48.2	57.7	82.0			
Basal area increments	A-gen	*stem number*	*45*	*44*	*45*	*40*	18.2	<0.001	59-64>[64-84/84-88] (Q≥3.34)**; 88-96>[64-84/84-88] (Q≥2.49)*
		median	41.4	11.0	0.0	24.3			
		average rank	109.6	73.9	70.6	96.7			
	B-gen	*stem number*	*37*	*30*	*37*	*39*	20.8	<0.001	59-64=88-96; 59-64>[64-84=84-88] (Q≥2.89)*; 88-96>[64-84=84-88] (Q≥3.19)**
		median	19.4	1.9	4.4	14.9			
		average rank	87.5	50.1	60.0	85.5			

(c) Correlation between increment rates for individual stems in successive periods

		A-generation (26 stems)		B-generation (22 stems)	
Periods	Rates compared	r_s	P	r_s	P
1959-64 v	Dbh increment	-0.098	ns	0.669	<0.001
1964-84	Basal area increment	-0.048	ns	0.386	<0.05
1964-84 v	Dbh increment	0.241	ns	0.435	<0.05
1984-88	Basal area increment	0.205	ns	0.481	<0.05
1984-88 v	Dbh increment	-0.130	ns	0.682	<0.001
1988-96	Basal area increment	-0.061	ns	0.720	<0.001

similarly high level during 1988-96. The rank dbh increment rates for individual oak trees between successive periods were never correlated in the A-generation, but were always significantly correlated in the B-generation (Table 3.1.19c).

Basal area increments were strongly related to initial basal area in all four study periods.

Table 3.1.20: Comparison of the increment rates over 1959-96 for oak stems in various crown position/size categories in 1996 in the permanent transect in Denny Inclosure. The table shows: (i) the median rate and average rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the average ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Dbh increment rates ($H_{df=4}$ = 20.4, P<0.001)

	n	median	average rank	pair-wise comparison of ranks
(a) Canopy with large/very large crown	9	0.239	44.4	=bcd; >e (Q=3.70)**
(b) Canopy with medium crown	19	0.225	42.6	=acd; >e (Q=4.13)***
(c) Canopy with small crown	17	0.185	38.4	=abd; >e (Q=3.53)**
(d) Canopy with very small crown	15	0.169	34.9	=abc; >e (Q=3.02)**
(e) Sub-canopy/understorey with small/very small crown	10	0.029	9.8	<abcd

(b) Basal area increment rates ($H_{(df=)}$ = 25.0, P<0.001)

	n	median	average rank	pair-wise comparison of ranks
(a) Canopy with large/very large crown	9	31.8	52.0	=bcd; >e (Q=4.47)***
(b) Canopy with medium crown	19	21.1	44.0	=acd; >e (Q=4.25)***
(c) Canopy with small crown	17	11.3	33.2	=abd; >e (Q=2.84)*
(d) Canopy with very small crown	15	15.4	34.3	=abc; >e (Q=2.90)*
(e) Sub-canopy/understorey with small/very small crown	10	1.4	10.2	<abcd

The regressions between increment and initial size were highly significant and accounted for 13-25% of the total variation, which increased to 29-52% if all stems with negative or zero increments were excluded (Table 3.1.18). In all periods there was a strong tendency for larger trees to have increased most and smaller trees least (Figure 3.1.13). Comparison for the rank increment rates for the two generations (Table 3.1.19a/b) revealed that: (i) the A-generation rates were significantly higher during 1959-64 and 1988-96 than throughout 1964-84-88; (ii) that the B-generation rates did not differ significantly over the four study periods; but (iii) that only during 1959- 64 did the A-generation rates significantly exceed the B-generation rates. Rank correlations between the basal area increment rates for individual trees in successive periods were never correlated for A-generation trees, but were always significantly correlated for B-generation trees (Table 3.1.19c).

3.1.2.4.3. Comparison of oak and beech growth

The average ranks of the dbh and basal area increment rates for the A- and B-generations of oak and beech were compared. For the dbh rates, only the B-generation average ranks

Figure 3.1.12: Relationships between the dbh increment and initial dbh for oak stems in the permanent transect in Denny Inclosure over (top left) 1959-64, (top right) 1964-84, (bottom left) 1984-88, and (bottom right) 1988-96. Parameters for the regression lines shown are given in Table 3.1.18. Some symbols represent more than one stem

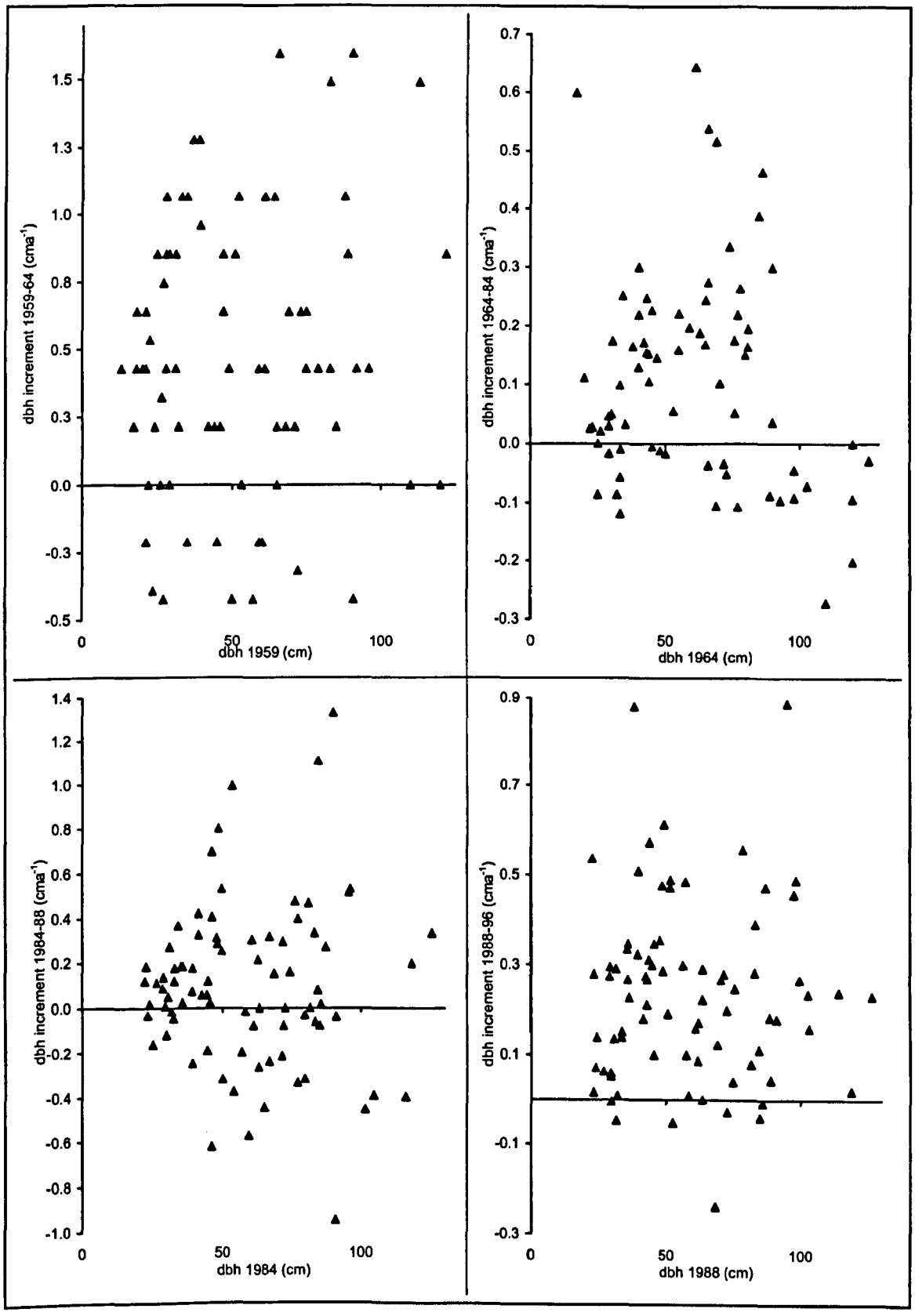
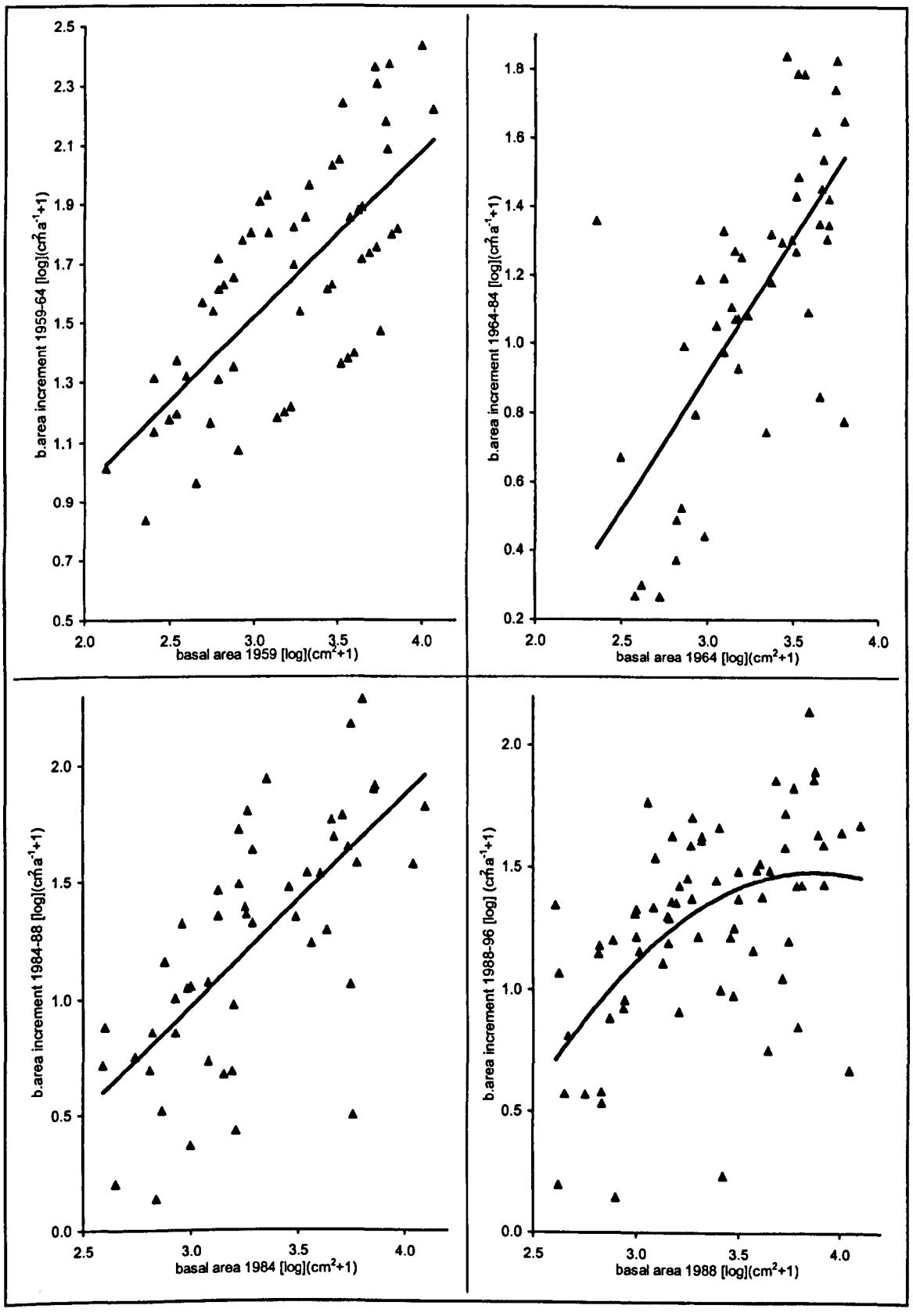


Figure 3.1.13: Relationships between the basal area increment and initial basal area for oak stems in the permanent transect in Denny Inclosure over (top left) 1959-64, (top right) 1964-84, (bottom left) 1984-88, and (bottom right) 1988-96. Stems with negative or zero increments were excluded. Parameters for the regression lines shown are given in Table 3.1.18. Some symbols represent more than one stem



differed significantly over the whole study period significantly, with beech exceeding oak (Table 3.1.21a). During the intervening periods there were other differences in the average ranks: (i) over 1959-64, the oak B-generation exceeded the beech B-generation; (ii) over 1964-84, the beech B-generation beech exceeded both oak generations, whilst the beech A-generation exceeded the oak B-generation oak; (iii) over 1984-88 there were no significant differences; and (iv) during 1988-96 the beech B-generation again exceeded both generations of oak. For the basal area rates (Table 3.1.21b), the only significant difference over 1959-96 was that the A-generation beech average rank was higher than the oak B-generation. During the intervening periods the average ranks differed only during 1959-64 (beech A-generation> oak B-generation; oak A- and B-generations>beech B-generation) and 1964-84 (beech A-generation> oak B-generation; beech B-generation>oak B-generation).

Table 3.1.21: Comparison of the stem increment rates for the beech and oak A- and B-generations in the permanent transect in Denny Inclosure during 1959-96. The tables show the median rates and average rank based on changes in stem dbh (cm a^{-1}) and basal area (cm^2 a^{-1}) and comparisons of the average rank based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant)

(a) Comparison of beech v oak dbh increment rates

Period		Beech A-gen	Beech B-gen	Oak A-gen	Oak B-gen	$H_{(df=3)}$	P	significant pair-wise comparison of ranks
1959-96	*stem number*	*33*	*139*	*36*	*33*			
	median	0.191	0.245	0.176	0.180	7.8	=0.05	beech B>oak B (Q=3.00)*
	average rank	121.0	130.5	100.5	103.3			
1959-64	*stem number*	*45*	*196*	*45*	*37*			
	median	0.638	0.213	0.426	0.426	28.6	<0.001	oak B>beech B (Q=4.41)***
	average rank	219.0	142.2	172.9	184.2			
1964-84	*stem number*	*40*	*144*	*44*	*30*			beech A>oak B (Q=2.91)*
	median	0.165	0.193	0.147	0.038	18.7	<0.001	beech B>oak B (Q=5.41)***
	average rank	131.1	144.6	105.3	90.4			beech B>oak A (Q=2.63)*
1984-88	*stem number*	*41*	*142*	*45*	*37*			
	median	0.000	0.207	0.000	0.111	13.1	=0.004	no differences between species
	average rank	108.1	148.1	113.2	126.8			
1988-96	*stem number*	*33*	*141*	*40*	*39*			
	median	0.187	0.291	0.191	0.275	22.3	<0.001	beech B>oak A (Q=3.50)**
	average rank	91.9	144.9	98.5	121.4			beech B>oak B (Q=2.59)*

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Table 3.1.21: continued

(b) Comparison of basal area increment rates

Period		Beech A-gen	Beech B-gen	Oak A-gen	Oak B-gen	$H_{(df=3)}$	P	significant pair-wise comparison of ranks
1959-96	*stem number*	*33*	*139*	*36*	*33*			
	median	21.9	11.3	18.3	10.5	23.7	<0.001	beech A>oak B (Q=4.78)***
	average rank	165.9	110.1	142.1	98.9			
1959-64	*stem number*	*45*	*196*	*45*	*37*			beech A>oak B (Q=4.37)***
	median	87.9	8.6	41.4	19.4	51.9	<0.001	oak A>beech B (Q=3.81)***
	average rank	236.2	135.3	199.0	167.9			oak B>beech B (Q=3.33)**
1964-84	*stem number*	*40*	*144*	*44*	*30*			
	median	16.6	7.9	11.0	1.9	10.9	=0.012	beech A>oak B (Q=4.15)***
	average rank	151.6	132.1	125.9	93.1			beech B>oak B (Q=3.93)***
1984-88	*stem number*	*41*	*142*	*45*	*37*			
	median	0.0	10.5	0.00	4.4	2.9	ns	no differences between species
	average rank	122.2	140.4	124.7	126.5			
1988-96	*stem number*	*33*	*141*	*40*	*39*			
	median	22.6	15.8	24.3	14.9	3.7	ns	no differences between species
	average rank	133.9	124.6	142.8	113.5			

3.1.2.4.4. Condition of oak in 1996

All live oak trees were given a crown position, size and die back category in 1996 (Table 3.1.22). 71 were placed in the canopy, of which 32 had medium or larger crowns, eleven were put in the sub-canopy and two in the understorey. Compared to beech, oak was less numerous in all layers and especially the lowest two, and had half the number of medium or larger crowned trees in the canopy.

Table 3.1.22: Stratification and crown condition of live oak trees in the permanent transect in Denny Inclosure in 1996. The table shows the number of stems in each category and the principal cause of deterioration for stems with severe or very severe die back (dr = drought; ex = excluded; wd = wind breakage; tip = tipped; ? = unsure)

Crown layer	Crown Size	Crown die back						Total
		None/part	Moderate	Severe		Very severe		
Canopy	Very large	1	1	-		-		2
	Large	7	1	-		-		8
	Medium	12	8	1	1dr?	1	1dr?	22
	Small	11	7	5	3wd, 2ex	1	1ex	24
	Very small	4	1	6	5ex, 1wd	4	2ex, 2dr?	15
Sub-canopy	Small	3	-	-		-		3
	Very small	-	-	3	3ex	5	2ex/tip, 1ex, 1wd, 1dr?	8
Under-storey	Small	-	-	-		1	1ex/wd	1
	Very small	-	-	1	1ex/wd	-		1
All	All	38	18	16		12		84

Severe or very severe die back was recorded on 28 oak trees, including most in the sub-canopy and understorey and 18 in the canopy (Table 3.1.22). The principle causes were: (i) exclusion – this affected 18 trees, including most in the sub-canopy and understorey, and

was mostly to do with competition from beech – several trees had become part-released with the stand opening up and showed some signs of recovery; (ii) wind damage (including breakages, tipping and strikes from other wind-damaged trees) – this affected nine trees, with storms of 1987 and 1990 probably being mainly responsible – again, several trees showed signs of recovery as they were vigorously producing epicormic shoots from the main trunk; and (iii) drought – this affected the crowns of five large trees and was characterised by otherwise inexplicable severe die back of canopy trees – it was probably related to the prolonged dry period from the mid-1970s.

3.1.2.5. Changes in the holly population from 1956-9 to 1996

3.1.2.5.1. Survival, mortality and recruitment patterns

There were 594 live standing holly stems, 15 live fallen holly stems, and 206 low-growing holly bushes in the 47 transect sections recorded in 1959. By 1996 this had changed to 168 live standing stems, 15 live fallen stems, and 107 low-growing bushes (Table 3.1.23). 73% of the original live stems had died or been reduced, and 73% of low-growing bushes had died. Nevertheless, 91 stems/low bushes managed to recruit giving a net population decline of 434 (53%). Of the 290 holly that survived throughout the 37 years: 66% remained in the same category; 3% of the taller stems toppled but remained alive; 7% grew over 1.3m in height (several of which then fell); and 24% were reduced from taller to low-growing.

Changes in holly stems ≥1.3m height/length were constructed for each of the four study periods (Table 3.1.24). As those reduced to low live growth (<1.3m tall) were mostly not recorded in 1984 and 1988, it was assumed that losses during 1964-84 and 1984-88 had died unless they persisted as low-growth in 1996. Stem mortality rates were high initially and remained moderate before falling sharply after 1988. Reduction rates were also high initially, but were generally low after 1964. Most stems reduced before 1964 died, whereas most reduced afterwards survived in a similar condition through to 1996. Recruitment rates

Table 3.1.23: Change in the holly population in the permanent transect in Denny Inclosure between 1959 and 1996. The table shows the fate of live holly stems (≥1.3m height/length) and low-growing holly individuals (<1.3m tall), and recruits by 1996 that were not present in 1959. Based on changes in 47 transect sections

1959		Fate by 1996			
Status	Number	Standing live stem	Fallen live stem	Low-growing individual	Dead
Standing live stem	594	154	10	71	359
Fallen live stem	15	-	-	-	15
Low-growing individual	206	14	5	36	151
Not present (recruits)	-	54	10	27	-
Total	815	222	25	134	525

Table 3.1.24: Fate and recruitment of live holly stems (≥1.3m height/length) in the permanent transect in Denny Inclosure in four periods between 1959 and 1996. Based on changes in 47 transect sections*

	1959-64		1964-84		1984-88		1988-96	
	standing stems	fallen stems	standing stems	fallen stems	standing stems	fallen stems	standing stems	fallen stems
Number at start	595	15	577	14	348	21	278	27
Condition at end								
No change	459	9	285	1	265	20	208	24
Toppled	4^{1S}	-	10^{6S}	-	2^{2S}	-	2	-
Reduced to low-growth	56^{9S}	-	28^{24S}	-	23^{23S}	-	31	1
Died completely	76	6	254	13	58	1	37	2
Recruits								
Not present at start	97	-	47	4	11	1	15	-
<1.3m tall at start	21	1	17	6	3	4	3	-
Rates ($n\ a^{-1}$)								
Mortality	17.4		13.0		14.8		4.9	
Reduction	11.9		1.4		5.8		4.0	
Recruitment	25.3		3.6		4.8		2.3	

^{S} = number in same condition in 1996; * section 24-25 was omitted in 1964, so it was assumed that all stems present maintained the same status in 1964 as recorded in 1959; section 25-26 was recorded only in 1958 and 1996, so the 1958 data was used for 1959 and it was assumed that the single live stem remained as such throughout and there was no recruitment in between

fell away sharply after 1964 and remained low. In every period, but especially during 1964-88, the rate of mortality and reduction combined exceeded the recruitment rate.

Stems that died or were reduced in 1959-64 and 1964-84 were predominately small-sized (Table 3.1.25), which implicated exclusion as the main process behind mortality. Thereafter losses were more evenly spread across the size-range and the main cause of

Table 3.1.25: Survival and mortality in relation to size for holly stems in the permanent transect in Denny Inclosure between 1959 and 1996. Size-classes are based on initial dbh in each period. The table shows the number of stems in each category. Based on all available transect sections for each period

	1959-64		1964-84		1984-88		1988-96	
Dbh (cm)	Survived	Died or reduced	Survived	Died or reduced	Survived	Died or reduced	Survived	Died or reduced
<5	103	87	40	143	65	4	63	13
5-<10	214	39	123	93	117	39	91	33
10-<15	116	10	92	36	69	26	50	15
15-<20	25	2	32	12	29	11	22	10
20-<25	7	-	5	8	4	2	6	-
25-<35	2	-	2	-	2	1	2	-

mortality/reduction appeared to be debarking and browsing by deer and ponies. These had certainly increased in numbers and in 1996 there was a distinct, head-height, browse-line through the area; 73 of the 89 snags present appeared to have been certainly killed by trunk debarking; and many stems remained alive but were badly debarked (see Figure 3.1.16).

Much of the holly population comprised individuals <1.3m tall. These grew as well-defined small bushes or patches of scrub covering $10m^2$ or more (the largest single patch covered $140m^2$ and carried out on outside the transect). Some patches broke up into separate clumps, some developed into taller individuals that usually retained a low-growing skirt of scrub, and some created when taller stems died off. This part of the population was recorded only in 1959, 1964 and 1996 (Table 3.1.26), and the accuracy of the 1959 and 1964 records was far from certain. They indicate that 1959-64 was a period of rapid turnover with 10% of the original low-growing individuals growing to 1.3m in height, 40% dying, and many recruiting from seedlings or taller individuals that were reduced. Low holly scrub cover within the transect declined from 3.9% to 2.4%, and the number of sections with 10% or more scrub cover declined from seven to four, indicating that large patches were breaking up. However, the decrease was not uniform: an increase in scrub cover was recorded in 13 sections compared to 22 sections in which it declined. This high turnover may well be an artefact of inaccurate nature of the records.

Table 3.1.26: Fate and recruitment of low-growing holly individuals (<1.3m height) in the permanent transect in Denny Inclosure during 1959-1964 and 1964-96. Based on changes in 46 transect sections*

Period	Number at start	Fate at end of period			Recruitment		Number at end
		No change	Grown to ≥1.3m tall	Dead	Stems ≥1.3 tall at start	Not present at start	
1959-64	208	104	21	83	52	60	216
1964-96	216	58	20	138	78	13	149

* section 24-25 was omitted in 1964, so it was assumed that all stems present in 1959 were the same in 1964

Holly scrub declined greatly during 1964-96 due to browsing by deer and ponies. The total cover declined to just 0.1% of the transect area and no section had more than 2% cover. The number of scrub patches declined by a third (Table 3.1.26): this would have been higher, but browsing and debarking reduced many taller stems to low-growth and this compensated for the high mortality of established scrub patches. Not surprisingly, far more individuals were browsed down and reduced by debarking than grew tall.

3.1.2.5.2. Growth of holly

Dbh increment over 1959-96 was best represented by a polynomial regression (Table 3.1.27, Figure 3.1.14). This demonstrated that middle-sized stems tended to have grown slightly faster than small and large stems, though the relationship was not strong. Dbh increments within periods were not related to size except during 1964-84, but again the relationship was weak. The average rank of the stem dbh increments differed significantly between the four study periods (Table 3.1.27a). It was high initially and during 1988-96, but was lower throughout 1964-84-88. The dbh increment rates in successive periods were rank correlated only between 1959-64 and 1964-84, with fast-grow stems tending to have grown slowest in the second period (Table 3.1.27b).

Basal area increments more strongly related to initial size (Table 3.1.27, Figure 3.1.11). The linear regression over 1959-96 accounted for 21% of the total variation and showed there was a strong tendency for larger individuals to have grown faster than smaller in both

Table 3.1.27: Results of the stem increment analysis for holly in the permanent transect in Denny Inclosure. The table shows the regressions comparing dbh increment (inc_{dbh}, cm a^{-1}) against initial dbh (ini_{dbh}, cm) and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2) during 1959-96. Lognormal data were transformed before analysis. Figure 3.1.14 show the 1959-96 relationships as scatter plots

(a) Dbh increment v initial dbh

Period	Dbh increment	n	F	P	r^2%
1959-96	$inc_{dbh} = -0.0003ini_{dbh}^2 + 0.0079ini_{dbh} + 0.0459$	129	3.8	=0.025	5.7
1959-64	no significant regression	347	-	-	-
1964-84	$inc_{dbh} = -0.0043ini_{dbh} + 0.0892$	187	7.3	=0.007	3.8
1984-88	no significant regression	121	-	-	-
1988-96	no significant regression	138	-	-	-

(b) Basal area increment v initial basal area

Period	Basal area increment	n	F	P	r^2%
1959-96	$\log(inc_{ba+1}) = 0.2136.\log(ini_{ba+1}) - 0.0171$	129	33.0	<0.001	20.6
1959-64	$\log(inc_{ba+1}) = 0.0993.\log(ini_{ba+1})^2 + 0.1070.\log(ini_{ba+1}) + 0.0467$	308	37.0	<0.001	19.5
1964-84	no significant regression	164	-	-	-
1984-88	$\log(inc_{ba+1}) = 0.7611.\log(ini_{ba+1}) - 1.1067$	85	17.7	<0.001	17.6
1988-96	$\log(inc_{ba+1}) = 0.3422.\log(ini_{ba+1}) - 0.0785$	134	32.4	<0.001	19.7

(c) Basal area increment v initial basal area (excluding all negative and zero increments)

Period	Basal area increment	n	F	P	r^2%
1959-96	as above	129	33.0	<0.001	20.6
1959-64	$\log(inc_{ba+1}) = 0.4034.\log(ini_{ba+1}) + 0.0399$	232	225.1	<0.001	49.5
1964-84	$\log(inc_{ba+1}) = 0.2367.\log(ini_{ba+1}) - 0.0783$	127	19.9	<0.001	13.7
1984-88	$\log(inc_{ba+1}) = 0.2876.\log(ini_{ba+1}) + 0.0260$	68	3.8	=0.057	5.4
1988-96	$\log(inc_{ba+1}) = 0.3713.\log(ini_{ba+1}) - 0.0706$	123	66.4	<0.001	35.4

Table 3.1.28: Comparison of the stem increment rates for holly in the permanent transect in Denny Inclosure during 1959-96. The tables show; (a) the median rate and average rank based on changes in stem dbh (cm a^{-1}) and basal area (cm^2 a^{-1}) and comparisons of the average rank based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple (Q) tests; and (b) a comparison of the individual increment rates in successive periods for stems that survived throughout and were reliably measured at each recording based on Spearman rank correlation (r_s) tests (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant)

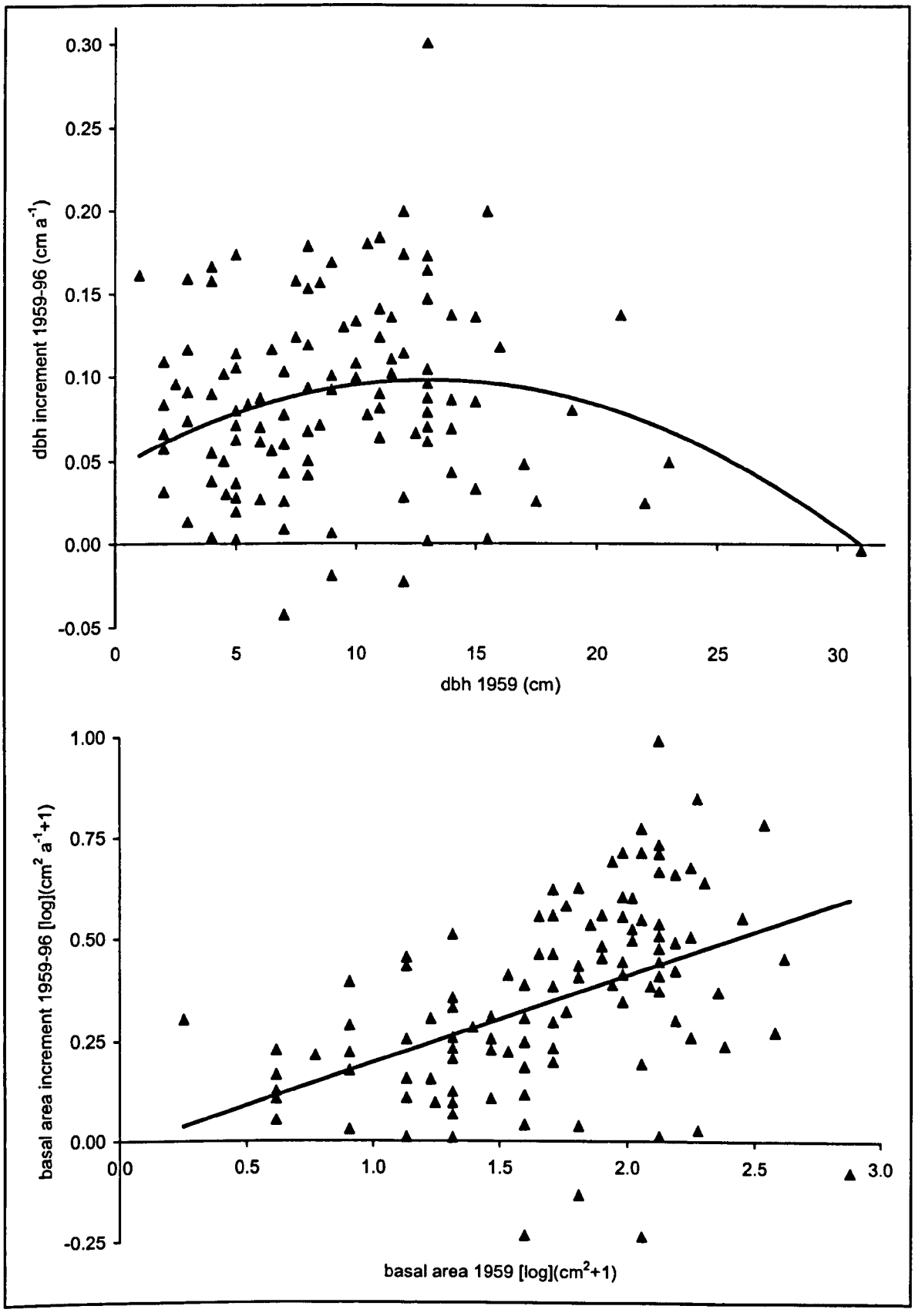
(a) Comparison of increment rates between each period

		1959-64	1964-84	1984-88	1988-96	H	P	significant pair-wise comparisons
Dbh increments	*stem number*	*347*	*187*	*121*	*138*	95.7	<0.001	[59-64=88-96]>[64-84=84-88] (Q≥6.13)***
	median	0.213	0.040	0.032	0.163			
	average rank	450.9	291.2	309.7	481.4			
Basal area increments	*stem number*	*347*	*187*	*121*	*138*	73.9	<0.001	88-96>[59-64/64-84/84-88] (Q≥3.82)***; 59-64>[64-84=84-88] (Q≥4.51)***
	median	2.17	0.55	0.43	2.74			
	average rank	432.2	304.9	328.2	493.4			

(b) Correlation between increment rates for individual stems in successive periods (n=68)

Periods	Rates compared	r_s	P
1959-64 v 1964-84	Dbh increment	-0.365	<0.01
	Basal area increment	-0.349	<0.01
1964-84 v 1984-88	Dbh increment	-0.081	ns
	Basal area increment	-0.038	ns
1984-88 v 1988-96	Dbh increment	0.055	ns
	Basal area increment	0.244	<0.05

Figure 3.1.14: Relationship between (above) the dbh increment and initial dbh and (below) the basal area increment and initial basal area of holly stems in the permanent transect in Denny Inclosure over 1959-96. Parameters for the regression lines shown are given in Table 3.1.27. Some symbols represent more than one stem



generations. Basal area increments were strongly positively related to initial basal area during 1959-64 and 1988-96, but were less so during 1964-84 and 1984-88, depending if all stems with negative or zero increments were excluded. A substantial number of holly stems apparently shrank between recordings: this is believed to related to the inaccurate measurement of such small, slow-growing stems surrounded by prickles and widespread removal of bark from the trunks (see Figure 3.1.16). The rank of the stem basal area increment rates also differed significantly over the four study periods (Table 3.1.28a). It was high initially, declined throughout 1964-84-88, and increased to its highest average during 1988-96. Individual stem increment rates were negatively rank correlated between 1959-64 and 1964-84, but positively rank correlated between 1984-88 and 1988-96 (Table 3.1.28b).

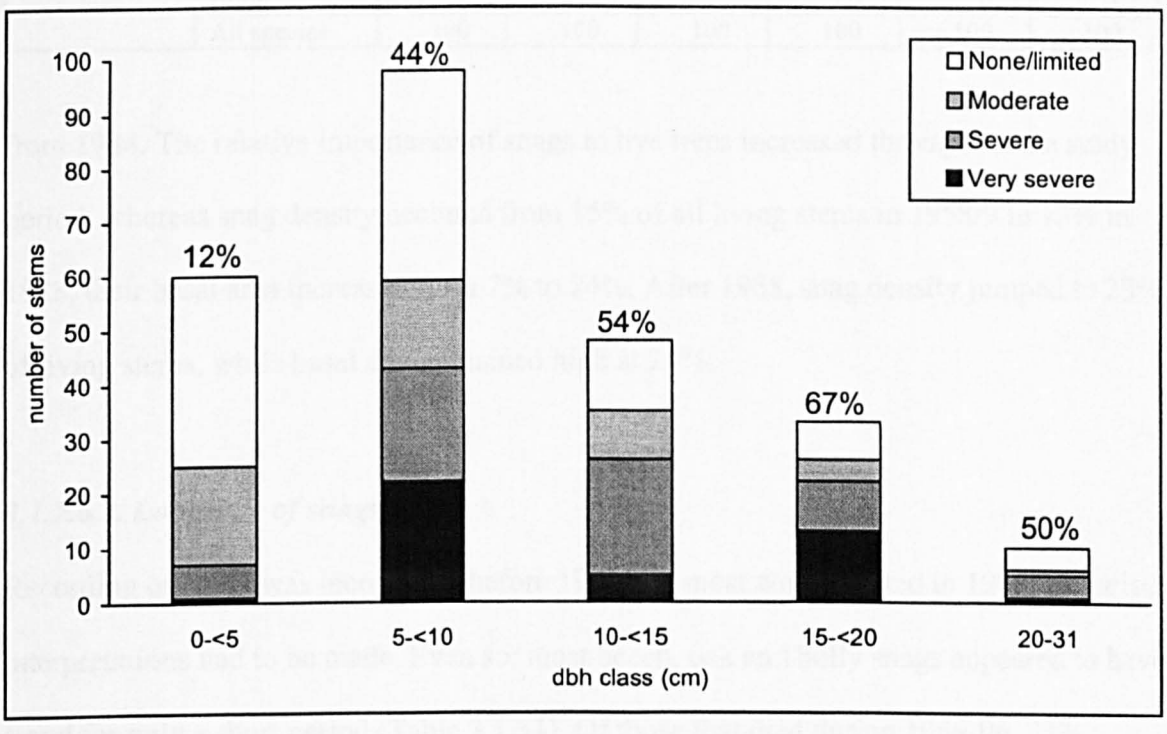
3.1.2.5.3. Condition of holly in 1996

Live holly stems in 1996 were categorised according to their crown position, crown size, amount of die back, and amount of trunk debarking by ponies/deer (Table 3.1.29, Figure 3.1.16). Most were placed in the understorey (n=241), but a few taller stems reached into the sub-canopy (n=8). Most (75%) crowns had little or no die back, but 18% had moderate and 7% had severe or worse die back mainly due to debarking. This was recorded on 213 of the 249 stems, of which 103 had been severely or very severely stripped, including 26 that had been ringed but were still alive. It occurred across the entire size range, but relatively few small stems <5cm dbh were badly affected (Figure 3.1.16). Most bark removal was confined to the lowest 2m of the trunk/low forks and particularly the zone between 0.5-1.3m, and many stems looked like they had been repeatedly debarked over many years. Evidently, ponies rather than deer gnawed most of them (Rory Putman, personal communication). Stems with severe or very severe debarking included 14 of the 17 with severe or very severe die back and 12 of the 34 with moderate die back. Nevertheless, 77 with this degree of debarking had little or no die back (Table 3.1.29).

Table 3.1.29: Stratification and crown condition of live holly trees in the permanent transect in Denny Inclosure in 1996. The table shows the number of stems in each category and (bracketed in superscript) the number with severe or very severe debarking

Crown layer	Crown size	Die back				Total
		None/part	Moderate	Severe	Very severe	
Sub-canopy	Small	$7^{(4)}$	-	-	-	7
	Very small	-	-	-	$1^{(1)}$	1
Understorey	Large	$10^{(4)}$	$1^{(1)}$	-	-	11
	Medium	$47^{(27)}$	$8^{(4)}$	-	-	55
	Small	$101^{(37)}$	$16^{(5)}$	$4^{(4)}$	$1^{(1)}$	122
	Very small	$21^{(5)}$	$21^{(2)}$	$2^{(1)}$	$9^{(7)}$	53
All	All	186	46	6	11	249

Figure 3.1.16: Trunk debarking by ponies/deer in relation to the size of live holly stems in the permanent transect in Denny Inclosure in 1996. The percentage of stems in each size-class with severe or very severe debarking is shown at the top of the column



3.1.2.6. Changes in dead wood from 1956-9 to 1996

3.1.2.6.1. General changes in snags

The density and basal area of snags changed over 1956-96 (Table 3.1.30). Although snags were probably under-recorded before 1964, it was clear that their initial density was high and during 1964-1988 they decreased in density and increased in basal area. Thus, there was a general change from many small snags to fewer, larger snags. Both trends were reversed after 1988. Whereas the relative importance of beech snags declined after 1984, oak importance fluctuated but overall changed little, and holly increased in importance

Table 3.1.30: Change in the basal area, density and relative importance snags recorded on the permanent transect in Denny Inclosure from 1956 to 1996. Includes all recorded dead standing stems ≥1.3m height. Relative importance = [% total basal area + % all stems]÷2

		1956	1958/9	1964	1984	1988	1996
Basal area (m^2 ha^{-1})	Beech	1.7	2.4	2.7	4.8	6.2	4.2
	Oak	1.4	1.6	2.0	1.4	3.0	2.5
	Holly	0.2	0.2	0.2	0.2	0.3	0.4
	Birch	0.1	0.1	0.1	0	0	0.1
	All species	3.4	4.2	4.9	6	10	7.3
Density (n ha^{-1})	Beech	55	56	53	21	16	20
	Oak	17	14	14	11	13	12
	Holly	29	35	32	26	22	46
	Birch	1	1	1	0	0	1
	All species	101	106	100	58	51	79
Relative importance (%)	Beech	52	55	54	58	47	41
	Oak	29	26	27	21	28	25
	Holly	17	19	18	24	23	32
	Birch	2	2	2	0	0	1
	All species	100	100	100	100	100	100

from 1984. The relative importance of snags to live trees increased throughout the study period: whereas snag density declined from 15% of all living stems in 1958/9 to 13% in 1988, their basal area increased from 7% to 24%. After 1988, snag density jumped to 23% of living stems, while basal area remained high at 20%.

3.1.2.6.2. Longevity of snags

Recording of snags was incomplete before 1996 and most were omitted in 1988, so various interpretations had to be made. Even so, most beech, oak and holly snags appeared to have stood for only a short period (Table 3.1.31). Of those that died during 1959-96, 71% appeared to have collapsed before the end of the period in which they died, despite most having probably died standing. Assuming they persisted/formed about half-way through each period, the average longevity of all that collapsed was just eight years. Generally, the smallest lasted the least time: 492 of the 697 that failed to form snags at the end of the period they died in were <10cm dbh, compared to only 107 of the 281 that did form snags ($\chi^2_{(df=1)} = 85.2$, $P<0.001$). Nevertheless, a few snags lasted for the full duration of the study and remained standing in 1996, including: (i) a 127cm dbh beech pollard that died during 1958-59; (ii) five 23-52cm dbh oak, of which four died sometime before and one during

Table 3.1.31: Longevity of beech, oak and holy snags in the permanent transect in Denny Inclosure between 1959 and 1996. The table shows the number of snags. Based on all available sections for each period

				Period when trees forming snags at end of period collapsed					
	Period	Number trees dying [a]	Collapsed before end of period	<1959	1959-64	1964-84	1984-88	1988-96	Still standing 1996
Beech A+B-gen	<1959	19	-	→	2	16[b]	-	-	1
	1959-64	17	5		→	11	1	-	-
	1964-84	59	31			→	10	8	10
	1984-88	19	6				→	7	6
	1988-96	29	17					→	12
Beech C-gen	<1959	87	6	→	47	40	-	-	-
	1959-64	58	27		→	30	1	-	-
	1964-84	127	119			→	4	4	-
	1984-88	15	12				→	2	1
	1988-96	15	6					→	9
Oak A+B-gen	<1959	26	-	→	4	16[c]	1	-	5
	1959-64	8	1		→	4	2	1	-
	1964-84	24	16			→	3	-	5
	1984-88	12	2				→	-	10
	1988-96	7	4					→	3
Oak C-gen	<1959	4	1	→	1	2[d]	-	-	-
	1964-84	2	1			→	1	-	-
Holly	<1959	131	66	→	34	29	-	-	2
	1959-64	138	112		→	26	-	-	-
	1964-84	295	260			→	16	2	14
	1984-88	82	52				→	2	25
	1988-96	71	26					→	45

[a] = number shown for <1959 includes any trees that were already dead when first recorded; [b] = includes two snags that were not recorded in 1964 but were assumed still standing; [c] = includes one snag that was not recorded in 1964 but was assumed still standing; [d] = both snags were not recorded in 1964 but were assumed to be still standing

1956-59; and (iii) two 5cm dbh holly that died during or before 1956-59, although these may have been confused with other stems between recordings and not lasted the full term.

3.1.2.6.3. Dead wood levels, dimensions and condition in 1996

Fallen dead wood was not assessed completely before 1996, though notes and sketches showed that a few fallen oak logs had survived since at least 1956. In 1996 the abundance, dimensions and condition of snags and fallen dead logs/branches was recorded in detail along the whole transect (Table 3.1.32). The combined volume and length of these was 278m^3 ha^{-1} and 5909m ha^{-1} respectively, much of which was lying on the ground.

Many snags were <25cm dbh, <7m tall and had little decay, but a substantial number of larger snags were present and about half retained a large amount of bark (Table 3.1.32).

Table 3.1.32: Quantity and condition of dead wood, including snags and all fallen dead logs/branches as recorded in the permanent transect in Denny Inclosure in 1996

	Snags				Fallen logs/branches		
	Beech	Oak	Holly	Birch	Beech	Oak	Holly
Volume (m^3 ha^{-1})	44.1	43.2	2.3	1.1	114.5	72.0	0.4
Length (m ha^{-1})	168	172	190	6	2859	2419	94
Density (n ha^{-1})	20	12	46	1			
Number recorded	39	23	89	1	91	77	3
Dbh (cm)							
0(snags)/5(fallen)-<10	1	-	46	-	36	28	2
10-<25	13	4	43	-	36	40	1
25-<50	13	12	-	1	15	5	-
50-82(fallen)/138(snags)	12	7	-	-	4	4	-
Height (m)							
0-2.5	10	1	24	-	-	-	-
3-7	12	5	58	-	-	-	-
>7	17	17	7	1	-	-	-
Decay state							
Solid	22	21	74	-	22	45	3
Part-rotten	6	1	5	1	52	26	-
Rotten	11	-	9	-	7	5	-
Very rotten	-	1	1	-	10	1	-
Remaining bark (%)							
0-<25%	15	13	26	-	50	47	2
25-<50%	3	1	18	-	14	1	-
50-<75%	9	3	20	-	14	6	-
75-100%	12	6	25	1	13	23	1

Most of the volume was split between beech and oak, but holly snags were frequent and accounted for 35% of the total length. Whereas: (i) most holly snags were <25cm dbh, <7m tall, had limited signs of decay and retained at least 25% of their bark; (ii) many oak snags were ≥25cm dbh and >7m tall, and most had limited signs of decay and retained little bark; and (iii) many beech snags were ≥25cm dbh, >7m tall, had much decay present and retained at least 25% of their bark.

Fallen logs/branches were relatively frequent and fairly evenly spread. Most were <25cm diameter at the point of intersection, had limited decay, and had lost at least half their bark (Table 3.1.32). Compared to snags, 114 out of 171 logs/branches had <50% bark whilst only 76 out of 152 snags did ($\chi^2_{(df=1)} = 9.2$, $P<0.01$). Beech and oak accounted for most of the snag volume and length, but beech was most abundant. Most beech logs appeared to be the product of either recent windstorms or residual from trees that died following the 1976

drought. Although some oak logs were also from recent windstorms, about two-thirds were long fallen (or fallen long dead) trunks, most of which showed no signs of decay. Indeed, 45 out of 77 oak logs were classed as solid compared to only 22 out of 91 beech logs ($\chi^2_{(df=1)} = 22.6$, $P<0.001$).

3.2. Stand change and natural disturbance at The Mens

3.2.1. Introduction

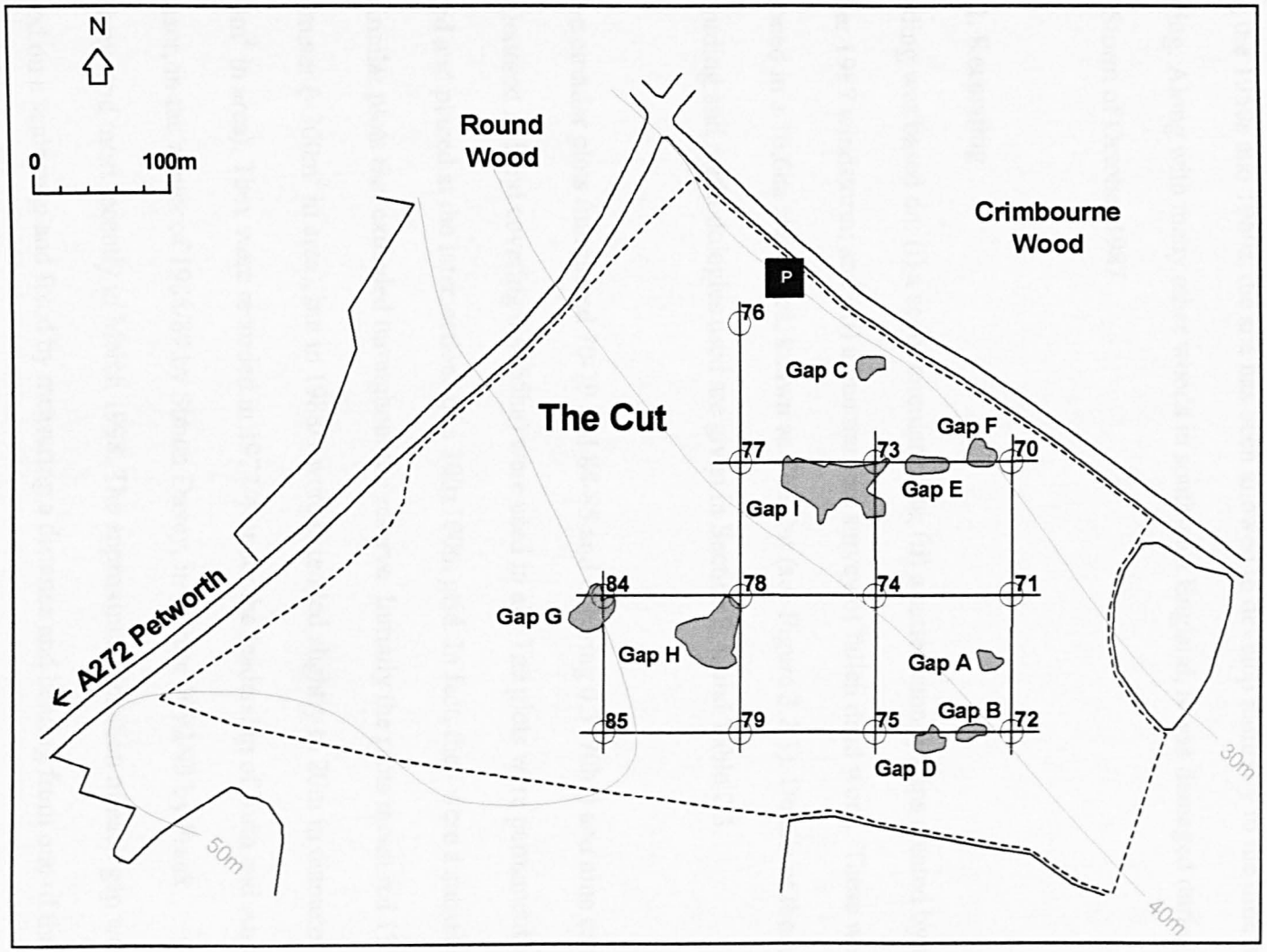
3.2.1.1. Site details

The Mens is located in West Sussex, south England (see Figure 2.1, Table 2.1). Tittensor & Tittensor (1977) and Tittensor (1978) give details of the site and its history, management, and flora and fauna. It forms one of the best and largest ancient, semi-natural, beech-oak woods in the English lowlands and accordingly is designated as a Site of Special Scientific Interest. It is owned and managed by Sussex Wildlife Trust under agreement with English Nature.

The reserve covers 155ha, within which the area of woodland known as The Cut (national grid reference TQ023236) was selected for study (Figure 3.2.1). This is sited on a gently undulating ridge at 30-50m above sea level. It is underlain by Wealden Clay and has mostly moderately acidic, slowly impermeable, stagnogleyic soils with a shallow mull humus, fine silty, clay-loam topsoil and clay subsoil. The area is covered by mature woodland, with beech and pedunculate/sessile oak dominating the canopy and holly, hazel and common and midland hawthorn the understorey (see Appendix for scientific names of species). A wide-range of minor trees and shrubs are present. The ground vegetation is generally sparse, except below large canopy gaps where bramble, bracken and honeysuckle can be abundant. The vegetation corresponds mostly to community W14 of the National Vegetation Classification (Rodwell 1991) and stand type 8B of Peterken (1993a).

The Mens is an ancient common, documented since 953AD with common rights for underwood and livestock grazing. In 1650, The Cut was shown as part-enclosed wood-pasture, combining open ground around scattered clumps of trees. In 1825 it was shown as the same, but in 1879 it was shown as closed woodland. This change was probably caused by enclosure: after 1773 various agreements were made to enclose and regenerate parts of

Figure 3.2.1: Site map showing the study area (dashed line, 16.6ha) and the twelve permanent circular plots and nine canopy gaps studied



The Mens, and some form of management (felling of timber trees, cutting and selling of underwood, replanting underwood, reserving timber trees) affected all parts some time during the 19th century. This period of silvicultural management came to an end following a ruling in 1882 that prevented further enclosure of the wood. From around the same time, livestock grazing declined as many of the grazing rights lapsed. Save for some thinning during the 1950s and 1960s, the site has been allowed to develop naturally to the time of recording. Along with many other woods in south-east England, it was damaged during the Great Storm of October 1987.

3.2.1.2. Recording

Recording was based on: (i) a set of circular plots; (ii) a series canopy gaps created by the October 1987 windstorm; and (iii) a line transect survey of fallen dead wood. These were positioned in a 16.6ha study area, known as The Cut (see Figure 3.2.1). Details of the aims of recording and methodologies used are given in Section 2.4. and Table 2.3.

Twelve circular plots (numbered 70-79 and 84-85 and covering 0.3770ha) and nine canopy gaps (lettered A-I and covering 0.4165ha) were used in all. The plots were permanently marked and placed at the intersections of a 100x100m grid. In fact, they were a subset of 155 circular plots that extended throughout the reserve. Initially the plots measured 19.54m in diameter (=300m^2 in area), but in 1988/9 were extended slightly to 20m in diameter (=314m^2 in area). They were recorded in 1972-4 under the leadership of Ruth and Andy Tittensor, in the winter of 1988/89 by Simon Davey, in Winter 1992/93 by Frank Docherty, and most recently in March 1998. The approximate location of each gap was marked on a scale map and fixed by measuring a distance and bearing from one of the permanent plot marker posts. They were recorded first by Tony Whitbread in spring 1988 and most recently March 1998. Details of the features recorded in the plots and gaps are shown in Table 3.2.1.

Table 3.2.1: Details of the records made in the permanent circular study plots and canopy gap study plots in The Mens

(a) Circular plot records

Date of recording	Features recorded
Between 1972-74	• Number of individuals ≥1.3m height for each species in each plot, divided into those in the tree layer (= largest live stem >20cm gbh) or shrub/sapling layer (= largest live stem >1.3m height and <20cm gbh) – taken from see Appendix 2 of Tittensor (2002)
Winter 1988-89	• All individuals ≥1.5m height, giving their location, species and status • Gbh of all the main stems, measured to the nearest cm – on multi-stemmed individuals, small girth stems and those <1.5m height were either counted or simply listed as 'subsidiaries' • Condition of selected individuals, making descriptive notes particularly of those with damage, covered by climbers, or which were sprouting from basal/epicormic shoots • Various salient features
Winter 1992-93	• Only plots 74-75 and 84 were re-recorded using the same methods as in 1988-89 and marking any losses and recruits
March 1998	• All individuals ≥1.3m height and all established seedlings (several years old and attaining 30cm height), including their location, species, and status (as standing alive, leaning alive, fallen alive, crown healthy, crown-dead, or dead) • Gbh of all live and dead stems ≥5cm gbh, to the nearest half cm • Condition of live stems, including notes on their form and debarking (with brief notes on smaller stems and seedlings and fuller descriptions for larger stems), allocation of a crown position and size, and scoring of debarking by grey squirrels, and cause of demise for stems that had been lost • Height and description of decay state for snags ≥20cm gbh • Extent of canopy gaps and notes on their origin and understorey infilling • Various salient features

(b) Canopy gap records

Date of recording	Features recorded
Spring 1988	• Extent of canopy gaps mapped onto a scale chart • Trees and shrubs ≥3m height within the gap, all wind-damaged individuals, and some around the gap margins, giving their location, species and status. • Gbh of the main stems on each individual, to nearest cm. • Condition of damaged individuals, making notes particularly of the crown condition, percentage crown loss, height of all major breaks, direction of fall of major branches, and size of root plates. • Various salient features.
March 1998	• Extent of canopy gaps mapped onto a scale chart and cause of any filling or further opening. • Condition of border/internal trees, including notes on losses, general condition of survivors, and scoring of grey squirrel bark-stripping damage. • Recruitment of trees ≥1.3m height and established seedlings (40-<130cm tall) and recruitment/expansion of shrubs, including approximate location and notes on condition. • Various salient features, including patches covered by dense ground vegetation. In addition, four larger gaps (E, F, G and H) were mapped in more detail using temporary transects and with the following were recorded: • All border and internal trees ≥1.3m in height (including recruits), giving their location, species and status. • Gbh of all live and dead stems on trees ≥1.3m height, to the nearest half cm – in Gap H the extent of dense shrub growth was mapped, noting the dominant species. • Condition of live stems, including descriptive notes and allocation of a crown position, crown size, scoring of grey squirrel bark-stripping damage, and height and decay state of snags. • Various salient features, including patches of dense ground vegetation and logs.

In addition, a line transect survey was undertaken in June 2001 to record the abundance and condition of fallen dead wood. This was done using ten 50m-long line transects, positioned at random within the vicinity of the circular plot/gap study area. Along these, the girth or diameter (to nearest cm) of all fallen dead stems ≥15cm girth was measured where they crossed the lines and notes made on their origin and condition.

3.2.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. Firstly, the analysis focused on the general changes in stand composition leading up to and just before the 1987 windstorm. Using the stand characteristics recorded in the twelve circular plots in 1972/4 and 1988/9: the latter was used to reconstruct the probable composition of the plots before the 1987 windstorm by assuming that certain dead or storm-damaged individuals were alive/upright before the storm struck. A more detailed analysis of the impact of the 1987 windstorm and changes to 1998 was made using both the circular plot and the canopy gap data, comparing features recorded in both 1988/9 and 1998 and by an assessment of the additional features recorded at the last date.

The data set provided information on 3915 stems/individuals/seedlings/seedling groups/ logs. A small number of mistakes and apparent errors were corrected for and various assumptions were made. The main problem was with the circular plot data and deciding how to deal the correspondence between the recordings, particularly because: (i) the plot size was increased from 19.54m to 20m diameter after 1972/4; (ii) it was possible that after 1972/4 slightly different positions were used for the plot centres; and (iii) the recording threshold for individuals changed from ≥1.3m height in 1972/4 and 1998 to ≥1.5m height in 1988/9 and 1992/3. In due course, it was assumed that a small number of trees were omitted from the 1972/4 record and several trees were best matched with large trees recorded just outside the plots later on. Similarly, there were problems matching up stems

that were listed only as 'subsidiaries' in 1988/9, and the gbh had to be estimated for all of these. Various standard measures were calculated and annual rates of change were based on: (i) (for the circular plots) 14 years for the period 1972/4 to winter 1987; one year for winter 1987 to winter 1988/9; and nine years for winter 1988/9 to spring 1998; and (ii) (for the canopy gaps) ten years for spring 1988 to spring 1998.

3.2.2. Results

3.2.2.1. Changes in the circular plots

3.2.2.1.1. Stand development before the 1987 windstorm

The circular study plots were located in stands that appeared to have regenerated from wood-pasture during 1825-1879. In 1972/4 they contained dense, high forest, with fourteen tree and shrub species represented (Table 3.2.2). The canopy was dominated by beech and oak, which accounted for 86% of individuals >20cm gbh. Beech was more numerous than oak and had a moderate number of small individuals present. A few larger birch and ash were recorded, but small individuals represented these moreover. Holly and hawthorn were most prolific amongst the shrubs, followed by hazel. All included a few larger individuals, but most were small. In addition, a few crab apple, elder, field maple, goat willow, wild cherry, wild service and yew were present, many of which were small.

Despite some problems matching up the 1972/4 data with the reconstructed composition of the circular plots in 1987, the correspondence generally appeared to be generally realistic. Between the two recordings, the density of all individuals combined had increased only slightly (Table 3.2.2). Beech and oak remained most numerous amongst the larger individuals, though oak declined more than beech and no small oak trees persisted. Ash and birch also declined, and the loss of 7 of the 11 original small birch was particularly severe. Holly, hawthorn and hazel remained the most numerous shrub species and all increased in large individuals. Whilst hawthorn and hazel changed little in overall density,

Table 3.2.2: Density (n ha^{-1}) of live individuals recorded in the twelve permanent circular plots in The Mens in 1972/4 and just before the 1987 windstorm. Sized was based on largest stem on each individual. The 1987 condition was reconstructed from records made in 1988/9. Includes all individuals ≥1.3m height in 1972/4 and ≥1.5m height in 1987

		1972/4		1987	
		Individuals >20cm gbh	Individuals ≤20cm gbh	Individuals >20cm gbh	Individuals ≤20cm gbh
Main tree species	Beech	222	72	207	50
	Oak	136	6	114	-
	Birch	8	31	8	11
	Ash	3	11	8	-
Shrubs/ medium trees	Holly	33	156	119	241
	Hawthorn	8	231	40	180
	Hazel	6	58	13	42
	Field maple	3	11	5	5
	Crab apple	3	-	3	-
	Wild service	3	-	3	-
	Wild cherry	-	17	-	-
	Yew	-	6	3	3
	Elder	-	3	-	-
	Goat willow	-	3	-	-
	All species	425	603	523	533

the number of holly doubled. In fact, holly increased by 4-11 individuals in six plots and by 29 in another, and very few individuals were lost. Hawthorn had a high turnover of individuals with 20 recruits and 23 losses: it also increased substantially in one plot, but in another it fell substantially. Similarly, hazel made 6 recruits but lost 8 individuals. All of the small elder, goat willow and wild cherry individuals were lost, but most field maple and all the crab apple, wild service and yew survived.

The reconstruction of the plots in 1987 provided a more detailed breakdown of initial stand composition (Tables 3.2.3-5). The mature character of the stands was reflected in the relatively high basal area (37m^2 ha^{-1}) and presence of several large trees up to a maximum of 291cm gbh. Oak and beech were the main canopy species, accounting for all large, most medium and some small-sized trees. Although beech stems were more numerous than oak, most were smaller girth and the basal area of oak exceeded beech. The very largest oak and beech were well-spaced trees, mainly standards but with a few old beech pollards. This

Table 3.2.3: Basal area, density and size-class distribution for live individuals/stems in the twelve permanent circular plots in The Mens just before the 1987 windstorm. Reconstructed from records made in 1988/9. Includes all individuals ≥1.5m height and all recorded stems ≥5cm gbh

					Gbh size-class (cm) (n stems)										
		Basal area (m^2 ha^{-1})	Individuals (n ha^{-1})	Stems (n ha^{-1})	5<10	10-<30	30-<50	50-<70	70-<80	90-<110	110-<130	130-<150	150-<190	190-<300	All sizes
Major trees	Oak	19.9	114	114	-	-	-	-	-	8	7	11	13	4	43
	Beech	14.5	257	313	11	24	28	19	15	6	6	4	2	3	118
Minor trees	Birch	0.1	19	19	1	4	1	1	-	-	-	-	-	-	7
	Ash	0.2	8	8	-	1	1	-	-	1	-	-	-	-	3
Major shrubs	Holly	1.5	361	395	62	56	27	4	-	-	-	-	-	-	149
	Hawthorn	0.6	220	337	66	52	9	-	-	-	-	-	-	-	127
	Hazel	0.2	56	119	17	28	-	-	-	-	-	-	-	-	45
Other species	Field maple	0.2	11	16	-	4	1	-	1	-	-	-	-	-	6
	Yew	<0.1	5	5	1	-	1	-	-	-	-	-	-	-	2
	Crab apple	<0.1	3	3	-	1	-	-	-	-	-	-	-	-	1
	Wild service	<0.1	3	3	-	1	-	-	-	-	-	-	-	-	1
	All species	37.3	1056	1332	158	171	68	24	16	15	13	15	15	7	502

Table 3.2.4: Summary description of the main components in the twelve permanent circular plots in The Mens (see text for details). The composition describes the status just before the 1987 windstorm struck, whilst canopy gaps were created later

Plot	Upper stratum	Lower stratum	Canopy gaps
70	Dominated by one large oak and one large beech; plus large oak just outside plot	Numerous suppressed beech; few birch, ash and cherry poles/saplings; some hazel; few holly, hawthorn and goat willow	Limited to edge part of a medium-sized 1987 storm gap, most of which was outside to the NW and by 1998 covered 6% of plot
71	Dominated by one large oak and one large beech; another oak, several beech and a birch present	Some holly and hawthorn; few hazel	Limited to part of a medium-sized 1987 storm gap to SE, which by 1998 covered 16% of plot but was mostly under-filled
72	Dominated by three large beech; three other beech, two oak and one ash present	Some hawthorn and holly; few hazel; single crab apple	Single gap covered <1% of plot in 1998, and large-sized 1987 storm gap outside to W
73	Dominated by one large oak and one large beech; another oak and four beech present	Numerous holly	Edge of 1987 storm gap to SW just into and covering <1% of plot in 1998
74	Dominated by one large oak; another oak and four beech present	Some holly and hawthorn; few hazel and yew	In 1998 a single gap covered 2% of plot
75	Dominated by one large oak and one large beech; four other oak and six beech present	Some holly; few hawthorn and hazel	Limited to three equal-sized 1987 storm gaps, which covered 17% of plot in 1998: one was rapidly infilling; one had infilled; and one was mostly under-filled
76	Dominated by three large oak; one other oak and two beech present	Numerous holly; abundant hawthorn; few hazel, field maple, birch and elder	Remained closed, but small-sized 1987 storm gap just outside to NE
77	Dominated by two large oak; another oak and two beech present	Numerous holly, and few hazel and hawthorn	Limited to single 1987 storm gap, which had covered about 5% of the plot but was infilled by 1998
78	Dominated by several large oak and beech	Several suppressed beech; abundant holly; some hawthorn; few hazel	Included NE edge of large-sized 1987 storm gap that was part-increased by later storms, and was 44% open and 29% under-filled in 1998
79	Dominated by several large oak and beech	Numerous suppressed beech poles; some hawthorn; few holly; single wild service	Two very small gaps covered <1% of plot in 1998
84	Dominated by mainly by large oak plus some beech	Abundant hawthorn; some holly; few hazel	Included N part of medium-sized 1987 storm gap that part-increased by later storms, and was 48% open and 7% under-filled in 1998
85	Dominated by three large oak and one large beech; three other oak and six beech present	Abundant hawthorn; few hazel, holly and field maple	Included a post-1987 storm gap on W side which covered 28% of plot in 1998 (7% was open and 21% under-filled), and a 1987 storm gap to E which was under-filled and covered 4% of plot in 1998

Table 3.2.5: Basal area, density and relative importance of live stems in the twelve permanent circular plots in The Mens just before the 1987 windstorm struck. Reconstructed from records made in 1988/9. Includes all recorded stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Basal area (m^2 ha^{-1})													
Beech	5.1	26.5	20.1	20.0	11.0	24.4	1.6	2.4	16.9	26.0	9.7	9.5	14.5
Oak	9.0	16.6	5.3	12.3	11.4	20.7	38.4	19.3	30.5	25.1	23.3	27.0	19.9
Ash	0.5	-	2.4	-	-	-	-	-	-	-	-	-	0.2
Birch	0.3	0.7	0.2	-	-	-	-	-	-	-	-	-	0.1
Holly	0.2	1.7	0.6	10.5	1.0	0.3	0.1	3.3	0.2	0.1	0.1	0.2	1.5
Hawthorn	<0.1	0.4	0.2	-	0.9	0.1	4.8	0.2	0.1	0.2	0.4	0.3	0.6
Hazel	0.4	0.3	0.6	-	-	-	0.4	0.4	-	-	-	0.2	0.2
Field maple	-	-	-	-	-	-	0.4	-	-	-	-	1.5	0.2
Yew	-	-	-	-	0.3	-	-	-	-	-	-	-	<0.1
Wild service	-	-	-	-	-	-	-	-	-	0.2	-	-	<0.1
Crab apple	-	-	0.1	-	-	-	-	-	-	-	-	-	<0.1
All species	15.6	46.1	29.6	42.9	24.6	45.5	45.7	25.6	47.6	51.9	33.8	38.7	37.3
Density (n ha^{-1})													
Beech	382	286	382	223	127	350	64	64	414	1050	191	223	313
Oak	32	64	64	64	64	159	127	95	191	159	159	191	114
Birch	159	32	32	-	-	-	-	-	-	-	-	-	19
Ash	64	-	32	-	-	-	-	-	-	-	-	-	8
Holly	191	446	255	1178	318	191	286	1178	255	127	223	95	395
Hawthorn	32	223	286	-	95	191	1369	95	255	414	477	605	337
Hazel	509	127	159	-	-	-	286	159	-	-	-	191	119
Field maple	-	-	-	-	-	-	32	-	-	-	-	159	16
Yew	-	-	-	-	64	-	-	-	-	-	-	-	5
Wild service	-	-	-	-	-	-	-	-	-	32	-	-	3
Crab apple	-	-	32	-	-	-	-	-	-	-	-	-	3
All species	1369	1178	1241	1464	668	891	2165	1592	1114	1783	1050	1464	1332

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Table 3.2.5: continued

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Relative importance (%)													
Beech	30	41	49	31	32	46	3	7	36	55	23	20	31
Oak	30	21	12	17	28	32	45	41	41	29	41	41	31
Ash	4	-	5	-	-	-	-	-	-	-	-	-	1
Birch	7	2	2	-	-	-	-	-	-	-	-	-	1
Holly	8	21	11	52	26	11	7	43	12	4	11	4	17
Hawthorn	1	10	12	-	9	11	37	3	12	15	23	21	14
Hazel	20	6	7	-	-	-	7	6	-	-	-	7	5
Field maple	-	-	-	-	-	-	1	-	-	-	-	7	1
Yew	-	-	-	-	5	-	-	-	-	-	-	-	<1
Wild service	-	-	-	-	-	-	-	-	-	1	-	-	<1
Crab apple	-	-	1	-	-	-	-	-	-	-	-	-	<1
All species	100	100	100	100	100	100	100	100	100	100	100	100	100

'A-generation' presumably represented surviving trees from the 17-18th century when the area was open parkland. Next, there was a 'B-generation' of medium-large oak and beech, possibly with a single ash and field maple, which were spread between the A-generation trees and presumably represented survivors that established after enclosure during 1825-79. They seemed to have developed naturally, though some might have been planted.

A scatter of oak stumps recorded across the circular plots showed that this generation had been thinned, most likely during the operations in the 1950s/60s (NB: stumps from beech cut at this time are unlikely to have persisted). Even so, oak was more numerous than beech in this generation in 1987. This and possibly earlier operations appeared to have facilitated a younger 'C-generation', as represented by smaller trees, mostly beech maidens or multi-stemmed coppice, plus a few maiden ash and birch, but no surviving oak.

The C-generation also included the main understorey shrubs, amongst which holly was most widespread and with the highest basal area and density of stems, including 31 stems of 30-60cm gbh (Tables 3.2.3-5). Hawthorn was almost as widespread, but was less frequent and few stems attained 30cm gbh. Hazel was much less widespread (having been excluded from several plots since 1972/4), and it had the lowest basal area with all of its stems being <30cm gbh. The size-distribution of holly and hawthorn stems indicated considerable recent recruitment, whereas the hazel distribution indicated this had been much more limited. In addition, the four minor species were represented by: (i) three field maple individuals divided between two plots, two of which were possibly derived from coppice; (ii) two 9-32cm gbh yew individuals in plot 74 (another occurred just outside plot 76); and (iii) a single wild service and crab apple sized 21-31cm gbh.

There was considerable variation in the composition of each plot (Tables 3.2.4-5). The basal area ranged from 15.6-51.9m^2 ha^{-1} and density from 668-2165 stems ha^{-1}. Variation

in basal area was mainly related to the abundance of medium-large beech and oak. Variation in the number of live stems was mostly due differences in the density of understorey shrubs. Seven plots (70, 71, 73, 74, 75, 78, 79) could be described as sub-equal mixtures of oak and beech; four (76, 77, 84, 85) as oak-dominated; and one (72) as beech-dominated. Holly made a major contribution to the basal area in plot 73 and was especially numerous in this and plot 77, whilst hawthorn made a notable contribution to the basal area in plot 76 where it was numerous. Only plot 70 had a notably low basal area: it had a 275cm gbh oak located just outside. This plot contained many of the small girth tree saplings, whilst plot 79 had many pole-sized beech present. Rank correlation testing indicated that beech had inhibited hazel in the understorey, with the basal area of beech being negatively correlated with the density of hazel stems ($r_{s(df=10)} = -0.583$, $P<0.05$), whilst the basal area of oak was positively correlated with the density of hawthorn stems ($r_{s(df=10)} = 0.683$, $P<0.05$), indicating these had persisted/developed best under oak.

Several snags were identified, though there was probably more. They included eight beech, seven hawthorn, and four each of hazel and oak. Most of these were <25cm gbh, but three of the beech were larger (45-68cm gbh) and four of the oak larger still (65-113cm gbh). Nevertheless, all had probably been excluded, as the larger snags were positioned next to large trees, mainly of beech. Thus, canopy gaps were probably scarce, though some small openings might have been residual from the thinning operations in the 1950s/60s.

3.2.2.1.2. Changes in canopy gaps during 1987-98

The October 1987 windstorm damaged several parts of the study area (Figure 3.2.1), and further localised windstorm damage occurred during 1988/9-98. Canopy gaps were not measured after the 1987 storm but in 1998 they averaged 17% across the circular plots. Even so, nine of the plots suffered little canopy disturbance and in 1998 had <20% gaps recorded (Table 3.2.4). Five of these (72, 73, 74, 76, 79) had remained more or less closed

throughout, whilst two (70, 77) had only very small openings in 1998, and the two others (71, 75) contained only small parts of larger gaps, which were created by the 1987 storm and had mostly infilled. Plot 79 did loose a 149cm gbh beech in the 1987 storm, but this did not leave much of a gap suggesting the tree had been in a poor state beforehand. The three other circular plots (78, 84, 85) had larger gaps covering >30% of the plots in 1998. Plot 78 was adjacent to the north end of canopy gap H and plot 84 was at the north end of canopy gap G (Figure 3.2.1). All three were all opened initially by the 1987 storm, but plots 78 and 84 were opened most and all lost canopy trees after the 1987 storm.

3.2.2.1.3. General changes in stem basal area and density during 1987-98

The 1987 windstorm blew down or resulted in the crushing of at least 80 stems in the circular plots. Others suffered substantial crown damage but were left standing alive (Section 3.2.3.1.4). However, only 19 had died by 1988/9 (Table 3.2.6), of which only four were large oak or beech trees. Thus, only in plots 78, 79 and 84 (where large trees were lost) was there an immediate substantial fall in basal area, and only in plots 71, 72 and 76 (where several small understorey stems were crushed) was there a moderate decline in stem density (Table 3.2.7). Although the average basal area and density of stems across the plots fell by only 4-5% by 1988/9, both declines were significant (paired-sample tests: $t_{\text{basal area (df=11)}} = 1.86$, $P = 0.04$; $t_{\text{stem density (df=11)}} = 3.27$, $P<0.01$). Beech and oak respectively accounted for 55% and 40% of the basal area lost, whereas the majority of stems lost were crushed hawthorn or hazel stems. Nevertheless, the relative importance of species was changed little (Table 3.2.7).

Only a few large trees died during 1988/9-98 (Table 3.2.6), though again several smaller stems were crushed and a few large trees suffered major crown damage but remained alive. The eight that died sized >50cm gbh were either beech or oak: some were damaged in the 1987 windstorm; some were damaged by later windstorms; and some were severely

Table 3.2.6: Fate, recruitment and cause of mortality for live individuals/stems in the twelve permanent circular plots in The Mens from just before the 1987 struck to 1998. The condition before the 1987 windstorm was reconstructed from records made in 1988/9. Includes all recorded individuals ≥1.5m height (1987) and ≥1.3m height (1998) and all stems ≥5cm gbh

	Number alive 1987	Fate by 1998			Cause of death						Recruits by 1998	Number alive 1998
		Survived	Died	Mortality rate (m%)	Died due to 1987 storm (dead by 1988/9)	Died due to 1987 storm (died after 1988/9)	Died due to later storm damage*	Died due to grey squirrel debarking*	Died due to exclusion*	Died due to other reasons*		
Individuals												
Beech	97	81	16	1.63	2	6	2	2	4	-	24	105
Oak	43	37	6	1.36	2	1	3	-	-	-	-	37
Ash	3	1	2	9.50	-	-	-	-	2	-	5	6
Birch	7	4	3	4.96	-	1	-	-	2	-	3	7
Holly	136	135	1	0.07	-	-	1	-	-	-	243	378
Hawthorn	83	79	4	0.45	1	3	-	-	-	-	10	89
Hazel	21	16	5	2.44	1	2	1	-	1	-	-	16
Field maple	4	4	-	-	-	-	-	-	-	-	-	4
Yew	2	1	1	6.11	-	-	-	-	-	1	-	1
Crab apple	1	-	1	all died	1	-	-	-	-	-	-	-
Wild service	1	1	-	-	-	-	-	-	-	-	-	1
All species	398	359	39	0.93	7	13	7	2	9	1	285	644
Stems ≥5cm gbh												
Beech	118	94	24	2.05	3	7	2	2	10	-	18	112
Oak	43	37	6	1.36	2	1	3	-	-	-	-	37
Ash	3	1	2	9.50	-	-	-	-	2	-	-	1
Birch	7	4	3	4.96	-	1	-	-	2	-	2	6
Holly	149	138	11	0.69	1	2	7	-	-	1	370	508
Hawthorn	127	105	22	1.71	7	6	3	-	6	-	87	192
Hazel	45	25	20	5.20	5	1	1	-	9	4	21	46
Field maple	6	6	-	-	-	-	-	-	-	-	-	6
Yew	2	1	1	6.11	-	-	-	-	-	1	-	1
Crab apple	1	-	1	all died	1	-	-	-	-	-	-	-
Wild service	1	1	-	-	-	-	-	-	-	-	-	1
All species	502	412	90	1.78	19	18	16	2	29	6	498	910

* died during 1988/9-98

Table 3.2.7: Change in the basal area, density and relative importance of live stems in the twelve permanent circular plots in The Mens from just before the 1987 windstorm struck to 1988/9. Condition before the 1987 windstorm was reconstructed from records made in 1988/9. Includes all recorded stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

(a) Change in basal area (m^2 ha^{-1}) from 1987 to 1988/9

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Beech	-	-0.16	-	-	-	-	-	-	-6.48	-5.62	-	-	-1.02
Oak	-	-	-	-	-	-	-	-	-4.48	-	-4.28	-	-0.73
Hazel	-	-0.06	-0.45	-	-	-	-	-	-	-	-	-	-0.04
Hawthorn	-	-0.11	-	-	-	-0.04	-0.18	-	-	-	-0.01	-	-0.03
Holly	-	-	-	-	-	-	-	-0.16	-	-	-	-	-0.01
Crab apple	-	-	-0.11	-	-	-	-	-	-	-	-	-	-0.01
All species	-	-0.33	-0.56	-	-	-0.04	-0.18	-0.16	-10.97	-5.62	-4.29	-	-1.84

(b) Change in stem density (n ha^{-1}) from 1987 to 1988/9

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Hawthorn	-	-64	-	-	-	-32	-95	-	-	-	-32	-	-19
Hazel	-	-32	-127	-	-	-	-	-	-	-	-	-	-13
Beech	-	-32	-	-	-	-	-	-	-32	-32	-	-	-8
Oak	-	-	-	-	-	-	-	-	-32	-	-32	-	-5
Holly	-	-	-	-	-	-	-	-32	-	-	-	-	-3
Crab apple	-	-	-32	-	-	-	-	-	-	-	-	-	-3
All species	-	-127	-159	-	-	-32	-95	-32	-64	-32	-64	-	-50

(c) Change in relative importance (%) from 1987 to 1988/9 (changes of <1% are not shown)

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Hazel	-	-	-6	-	-	-	-	-	-	-	-	-	-
Beech	-	-	+3	-	-	-	-	-	-4	-3	+3	-	-
Hawthorn	-	-2	+2	-	-	-1	-1	-	-	-	-	-	-
Crab apple	-	-	-1	-	-	-	-	-	-	-	-	-	-
Oak	-	-	-	-	-	-	-	-	+2	+3	-3	-	-
Holly	-	+2	+2	-	-	-	-	-	-	-	-	-	-

NB: for ash, birch, field maple, wild service and yew there was no change in basal area or stem density and no or only a minor change in relative importance

Table 3.2.8: Change in the basal area, density and relative importance of live stems in the twelve permanent circular plots in The Mens from 1988/9 to 1998. Includes all recorded stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

(a) Change in basal area (m^2 ha^{-1}) from 1988/9 to 1998

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Ash	-0.48	-	0.23	-	-	-	-	-	-	-	-	-	-0.02
Hazel	0.12	-0.08	-0.13	-	-	-	-0.03	-0.23	-	-	-	0.20	-0.01
Birch	0.04	0.08	-0.23	-	-	-	-	-	0.03	-	-	-	-0.01
Wild service	-	-	-	-	-	-	-	-	-	0.02	-	-	<0.01
Yew	-	-	-	-	0.06	-	-	-	-	-	-	-	<0.01
Field maple	-	-	-	-	-	-	0.11	-	-	-	-	0.13	0.02
Oak	0.10	1.28	0.16	1.89	0.85	2.00	3.85	1.35	-1.77	2.00	-9.31	-1.69	0.06
Hawthorn	-	0.10	0.09	-	-0.02	0.14	-0.30	-0.13	0.18	0.06	0.70	0.29	0.09
Holly	0.17	0.38	-0.03	-0.33	0.23	0.72	0.80	1.06	2.71	0.08	0.54	0.14	0.54
Beech	2.19	3.63	2.64	0.63	1.60	0.49	0.85	0.57	2.38	0.62	-0.69	0.07	1.25
All species	2.14	5.40	2.72	2.20	2.72	3.34	5.27	2.62	3.52	2.78	-8.75	-0.87	1.93

(b) Change in stem density (n ha^{-1}) from 1988/9 to 1998

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Oak	-	-	-	-	-	-	-	-	-32	-	-64	-32	-11
Beech	32	-64	-32	-95	-	318	-	-	32	-191	-32	-64	-8
Ash	-64	-	-	-	-	-	-	-	-	-	-	-	-5
Birch	-64	-	-32	-	-	-	-	-	64	-	-	-	-3
Yew	-	-	-	-	-32	-	-	-	-	-	-	-	-3
Hazel	-	-	-32	-	-	-	95	-64	-	-	-	159	13
Hawthorn	-	95	127	-	-32	318	-	32	159	64	987	541	191
Holly	127	318	159	573	668	1178	1178	1019	5411	159	6-5	64	955
All species	32	350	191	477	605	1814	1273	987	5634	32	1496	668	1130

(c) Change in relative importance (%) from 1988/9 to 1998 (changes of <1% are not shown)

	Plot 70	Plot 71	Plot 72	Plot 73	Plot 74	Plot 75	Plot 76	Plot 77	Plot 78	Plot 79	Plot 84	Plot 85	All plots
Beech	+5	-5	-3	-5	-4	-9	-	-	-13	-7	-1	-4	-5
Oak	-3	-1	-1	-	-3	-6	-2	-2	-12	-	-14	-4	-4
Hawthorn	-	+2	+3	-	-5	-	-13	-	-9	+2	+8	+7	-2
Hazel	-	-1	-2	-	-	-	-1	-4	-	-	-	+2	-2
Ash	-4	-	-	-	-	-	-	-	-	-	-	-	-
Birch	-2	-	-2	-	-	-	-	-	-	-	-	-	-
Yew	-	-	-	-	-3	-	-	-	-	-	-	-	-
Field maple	-	-	-	-	-	-	-	-	-	-	-	-1	-
Holly	+5	+6	+4	+4	+15	+15	+16	+7	+34	+4	+7	-	+13

NB: There was no change in the basal area of crab apple, nor the stem density of field maple and wild service, and only a minor change in the relative importance of wild service

debarked by squirrels (Section 3.2.2.1.4). Although oak accounted for the four largest losses, basal area loss was greater in beech that had 21 stems die. Three of the large losses were in plot 84, which consequently suffered a substantial decline in basal area (Table 3.2.8). Most plots, however, increased in basal area due to growth and/or recruitment of new stems. Indeed, the average basal area per plot increased significantly (paired-sample test: $t_{(df=11)} = 1.79$, $P = 0.05$), to a level almost identical to before the 1987 storm struck. Most of the basal area increase was due to changes in beech and holly.

Stem losses during 1988/9-98 were relatively limited, though total number lost was higher than just after the 1987 windstorm (Table 3.2.6). This was partly due to the delayed mortality of stems damage in the 1987 storm, but which took several years to die off. Overall, only 90 of the 502 stems ≥5cm gbh before the storm had died by 1998, giving a mortality rate (m) of 1.78% a^{-1}. Of these only 37 were adjudged to have been victims of the 1987 storm (m = 0.69% a^{-1}). Mortality was spread across the size-ranges up to 170cm gbh and particularly affected trees of 10-60cm gbh and 120-170cm gbh: but none larger died (Table 3.2.9).

Table 3.2.9: Mortality rate (m % a^{-1}) for stems of different sizes in the twelve permanent circular plots in The Mens from just before the 1987 windstorm struck to 1998. Includes all live stems ≥5cm gbh. Some size-classes were not represented (-)

Gbh size-class (cm)	Beech	Oak	Holly	Hawthorn	Hazel	All species
5-<10	2.85	-	0.45	1.01	2.41	1.16
10-<20	2.17	-	0.28	3.19	7.00	2.53
20-<40	4.03	-	1.15	1.55	8.53	2.61
40-<60	2.46	-	2.01	0.00	-	2.13
60-<80	0.63	-	0.00	-	-	0.52
80-<100	0.67	3.62	-	-	-	1.07
100-<120	0.00	0.95	-	-	-	0.63
120-<170	2.26	1.90	-	-	-	2.01
170-<300	0.00	0.00	-	-	-	0.00

Recruitment of new trees/stems after the storm far exceeded the losses, so stem density increased in all plots by 1998 (Table 3.2.8). The average rise of 1130 stems ha^{-1} per plot was significant (paired-sample test: $t_{(df=11)} = 2.56$, $P = 0.01$). Indeed, the average density went to almost twice that recorded before the 1987 storm struck. Most recruiting stems were holly, followed by hawthorn and then hazel and beech. In addition, a few new ash and birch individuals established (Table 3.2.6). The wave of holly recruitment was a key factor in the increase in the relative importance of holly (Table 3.2.8).

3.2.2.1.4. Changes amongst individual species during 1987-98

3.2.2.1.4.1. Oak

During 1987-98, six of the 43 oak in the circular plots died (Table 3.2.6). These were located in the three plots (78, 84, 85) where large gaps were recorded in 1998 (Table 3.2.4). They ranged from 98-148cm gbh and were amongst the 27 oak of <150cm gbh in 1987, i.e. all 16 larger oak survived (Table 3.2.9). All died due to windstorm damage, with most being broken rather than uprooted. Death was progressive: one tree was wind-snapped and another was windthrown/crushed in the 1987 windstorm and died immediately; another that was also wind-snapped in 1987 but died several years later; and the other three were wind-snapped after 1988/9 and were dead in 1998.

Sub-lethal storm damage was recorded on 15 of the 37 surviving oak in 1998. These were spread through most of the plots and included trees of 103-233cm gbh. Nine had suffered major snapping, whilst the others had lost only a minor part of their crown. Most damage appeared to be from the 1987 windstorm, including a single tree that was thrown over in 1987 and remained alive, but some were certainly snapped afterwards. Several trees were resprouting and the fallen oak had developed a colonnade of vigorous erect trunk shoots. Nevertheless, growth over 1988/9-98 was generally poor for trees with major crown loss

(Figure 3.2.2), and some appeared to have been permanently relegated and looked set to be excluded if the canopy closed in.

No oak recruitment was recorded, but three, 40-70cm tall, oak seedlings established below a canopy gap towards the centre of plot 78. Two were deer-browsed and none vigorous.

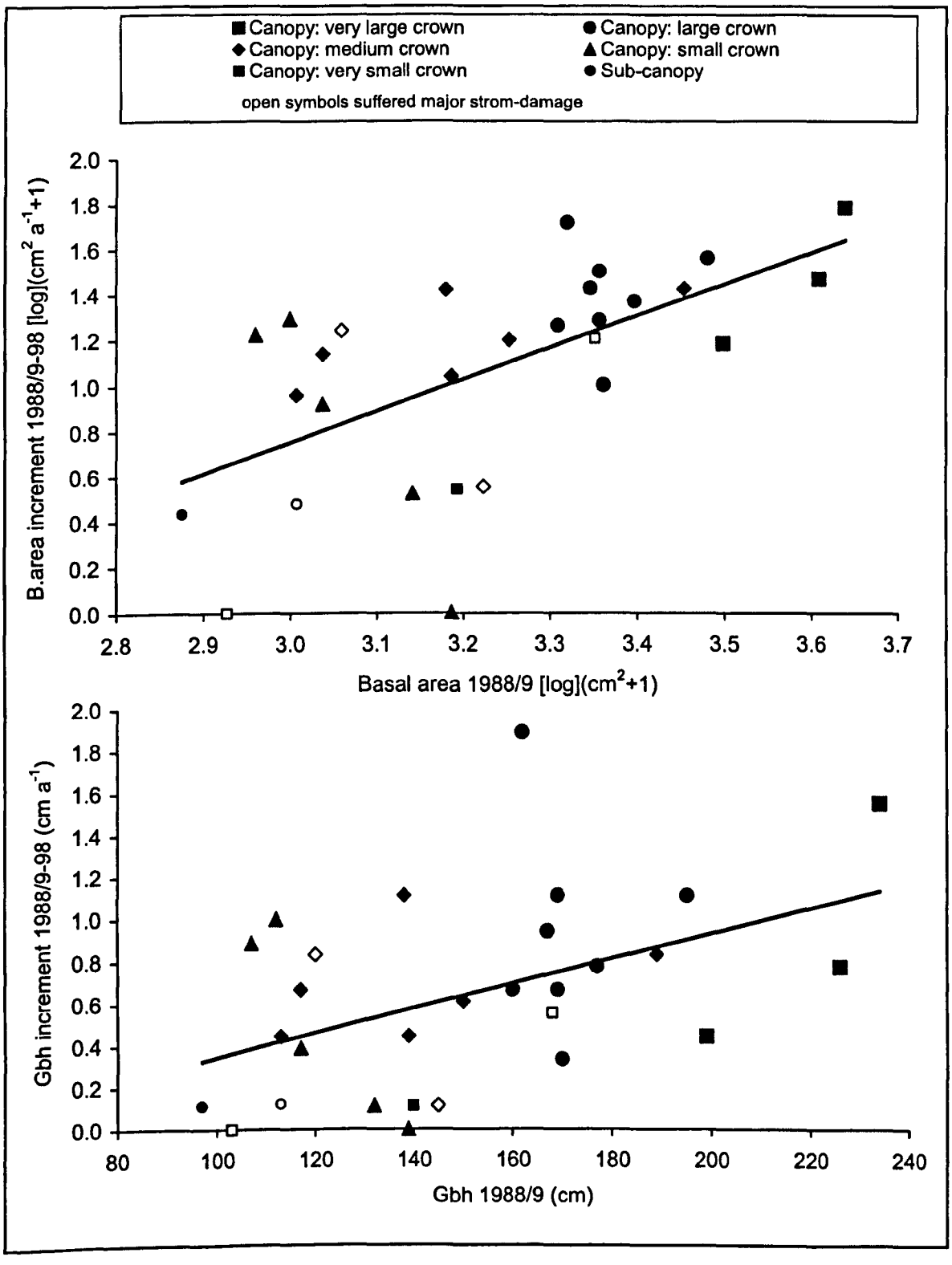
Oak stem gbh and basal area growth over 1988/9-98 was generally higher for the largest sized trees, which were predominately medium to very large-crowned trees in the canopy (Figure 3.2.2). Indeed, the median gbh/basal area increment rate for stems in the canopy with medium or larger crowns (0.78cm a^{-1}, 18.2cm^2 a^{-1}, n = 19) was significantly higher than for other stems (0.11cm a^{-1}, 2.4cm^2 a^{-1}, n = 10) (Mann-Whitney two-sample rank tests, $U = 344_{gbh}, 355_{basal\ area}$, P = 0.007, 0.001).

Despite widespread wind damage oak remained dominant amongst the larger crowned canopy trees in 1998 (Table 3.2.10). In addition, all 22 surviving medium or larger crowned canopy oak appeared healthy, only three had suffered major crown loss, and several showed signs of release with vigorous crown and/or sprout growth into gaps.

Table 3.2.10: Crown position and crown size for all live stems ≥5cm gbh in the twelve permanent circular plots in The Mens in 1998. The table shows the number of stems in a particular category

	Canopy					Sub-canopy			Under-storey
	Very large	Large	Medium	Small	Very small	Medium	Small	Very small	All
Oak	3	8	11	6	5	1	2	-	1
Beech	2	4	9	8	8	6	19	17	39
Ash	-	-	1	-	-	-	-	-	-
Birch	-	-	-	-	1	-	1	-	4
Holly	-	-	-	-	-	-	-	-	508
Hawthorn	-	-	-	-	-	-	-	-	192
Hazel	-	-	-	-	-	-	-	-	46
Field maple	-	-	-	-	-	-	1	-	5
Wild service	-	-	-	-	-	-	-	1	-
Yew	-	-	-	-	-	-	-	-	1
Total	5	12	21	14	14	7	23	18	796

Figure 3.2.2: Growth of oak stems in the twelve permanent circular plots in The Mens between 1988/9 and 1998. The relationships between (above) the basal area increment (inc_{ba}) and initial basal area (ini_{ba}) and (below) the gbh increment (inc_{gbh}) and initial gbh (ini_{gbh}) of stems are shown. The regression line equations are: $\log(inc_{ba+1}) = 1.3863.\log(ini_{ba+1}) - 3.4076$, n =29, F = 15.8, P<0.001, $r^2 = 36.9\%$; $inc_{gbh} = 0.0059.ini_{gbh} - 0.2492$, n =29, F = 7.4, P = 0.012, $r^2 = 21.4\%$



3.2.2.1.4.2. Beech

16 of 97 beech individuals and 24 of 118 beech stems died in the circular plots during 1987-98. This meant beech had a higher mortality rate than oak (Table 3.2.6). Losses were spread through most plots and ranged from 5-160cm gbh. Size-class mortality rates were highest for stems <60cm gbh and only four trees larger than this died (Table 3.2.9). Only three stems were killed immediately by the 1987 windstorm, but seven more damaged by the storm died by 1998. These included two trees of 50-160cm that were windthrown, a 149cm gbh tree that was wind-snapped, and six 25-86cm gbh trees that were struck, of which one snapped off and five were toppled completely. In addition, windstorm damage after 1988 snapped and killed a 73cm beech, and crushed a 20cm sub-canopy beech pole that also died. Ten other small-medium beech stems were excluded during 1988-98, and squirrel debarking killed two of 23-59cm gbh.

Only three surviving canopy beech had significant windstorm damage, two having lost a major part of their crown. In addition, two sub-canopy trees were leaning heavily and four sub-canopy and four understorey stems had had their tops snapped off: many of these had certainly been struck by canopy debris, but at least a few larger stems might have been debarked by grey squirrels at the point of breakage beforehand. Another 42cm gbh stem had been windthrown and left with a poor crown, though one vigorous trunk sprout close to the base had started to grow up.

In addition, half of the live beech stems in 1998 had been debarked by grey squirrels, albeit that much of the damage was small-scale (Table 3.2.11). In fact, most small and large stems remained unscathed and the worst damage was found mainly on medium-sized, 60-<120cm gbh stems, several of which had suffered major crown loss. This damage was in addition to the two 23-59cm gbh trees killed by squirrel debarking (Table 3.2.6). Stems that had grown rapidly tended to be preferentially selected for debarking (Figure 3.2.3).

Table 3.2.11: Grey squirrel debarking to live beech stems in the twelve permanent circular plots in The Mens in 1998. The relationship between stem size and the degree of debarking is shown, with the number of stems given for each category

	Maximum debarking category				
Gbh (cm)	None	Limited	Moderate	Severe	Very severe
5-<20	29	4	-	-	1
20-<40	11	2	1	-	-
40-<60	10	7	-	2	-
60-<80	4	4	2	1*	2*
80-<100	1	6	-	3*	3*
100-<120	-	3	2	2*	-
120-<140	-	3	1	-	-
140-<310	1	7	-	-	-
All stems	56	36	6	8	6

* combining stem numbers in each size-class, severe/very severe damage was found to be strongly associated with stems of 60-<120cm gbh ($\chi^2_{(df=1)} = 18.6$, $P<0.001$)

Beech stem gbh and basal area growth over 1988/9-98 was positively related to the initial size of stems, with the basal area regression proving particularly strong (Figure 3.2.3). The fastest-grown trees had large or very large crowns in the canopy, but rates for canopy trees varied considerably. Several sub-canopy trees also grew rapidly, probably because they had been released into canopy gaps, but many in the lower canopy layers grew little. Comparison of the rank increment rates showed that trees that ended up in the canopy generally grew at similar rates regardless of crown size, but these generally grew faster than trees that ended up in the sub-canopy/understorey (Table 3.2.12).

Beech recruited 24 new individuals and 18 stems (which grew to 5cm gbh or more) (Table 3.2.6). Many of the stems that reached 5cm gbh were weak, basal sprouts/low trunk shoots on existing trees or (most often) broken stems or stumps. However in the well-lit conditions of plot 78, 21 new saplings arose, strong growth developed from an old stump, and 78 small beech seedlings established, of which 21 had reached 1-1.2m tall and only 19 were part-browsed. Only a few beech seedlings recruited or established elsewhere.

By 1998, beech was slightly less numerous in the canopy than oak but it was more frequent

Figure 3.2.3: Growth of beech stems in the twelve permanent circular plots in The Mens between 1988/9 and 1998. The relationships between (above) the basal area increment (inc_{ba}) and initial basal area (ini_{ba}) and (below) the gbh increment (inc_{gbh}) and initial gbh (ini_{gbh}) of stems are shown. The regression line equations are: $\log(inc_{ba+1}) = 0.1625.\log(ini_{ba+1})^2 - 0.1383.\log(ini_{ba+1}) + 0.1682$, n =84, F = 71.6, P<0.001, $r^2 = 63.9\%$; $inc_{gbh} = 0.0048.ini_{gbh} + 0.4157$, n =84, F = 15.3, P< 0.001, $r^2 = 15.7\%$

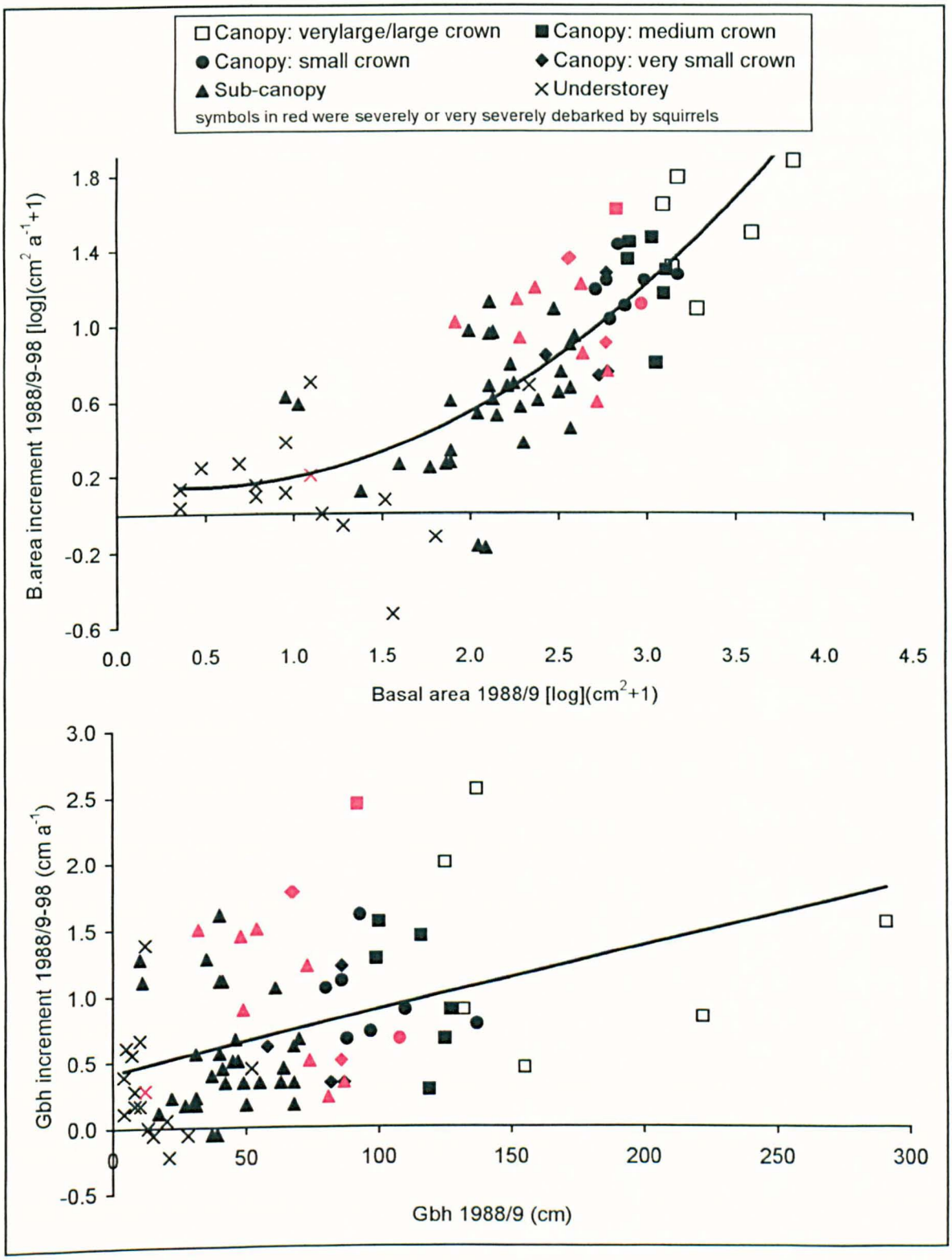


Table 3.2.12: Comparison of the increment rates over 1988/9-98 for beech stems in various crown position/size categories in the twelve permanent circular plots in The Mens in 1998. The table shows: (i) the median rate and mean rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the mean ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05, (*) = P<0.05)

(a) Gbh increment rates ($H_{(df=3)}$ = 27.3, P<0.001)

	n	median	mean rank	pair-wise comparison of ranks
(a) Canopy with medium, large or very large crown	13	1.28	63.0	=b; >c (Q=2.66)*, >d (Q=4.72)***
(b) Canopy with small or very small crown	15	0.78	55.3	=ac; >d (Q=3.98)***
(c) Sub-canopy all crown sizes	40	0.47	38.8	<a; =bd
(d) Understorey all crown sizes	16	0.22	23.2	<ab; =c

(b) Basal area increment rates ($H_{(df=3)}$ = 54.8, P<0.001)

	n	median	mean rank	pair-wise comparison of ranks
(a) Canopy with very large, large or medium, crown	13	26.5	73.5	=b; >cd (Q≥4.06)***
(b) Canopy with small or very small crown	15	14.2	62.0	=a; >c (Q=2.91)*, >d (Q5.29)***
(c) Sub-canopy all crown sizes	40	3.6	36.5	<ab; >d (Q=2.51) (*)
(d) Understorey all crown sizes	16	0.3	14.1	<abc

in the sub-canopy and understorey (Table 3.2.10). Several trees showed signs of growth release with vigorous crown growth and/or trunk/bough sprouts growing into canopy gaps.

3.2.2.1.4.3. Birch

Of the seven live birch trees in 1987, the second largest died after being bent over by a large beech windblown in the 1987 windstorm and the two smallest were excluded by 1998 (Table 3.2.6). This left: (i) two suppressed 14-18cm gbh saplings; and (ii) two part-released of 30-55cm gbh. In plot 78, birch recruited three saplings (two were growing vigorously) and had four, browsed, 40-80cm tall seedlings establish.

3.2.2.1.4.4. Ash

Both of the small ash poles were excluded by 1998, but the 102cm gbh tree survived as a medium-crowned, canopy tree (Table 3.2.6). Below the gap in plot 84, five 1.3-2.5m tall ash saplings had recruited amongst a pile of fallen trunks in moderately well-lit conditions. They were from a dense cohort of 60 plus seedlings first recorded in 1992, which had established in the northern part of a medium-sized gap, created by the 1987 windstorm and

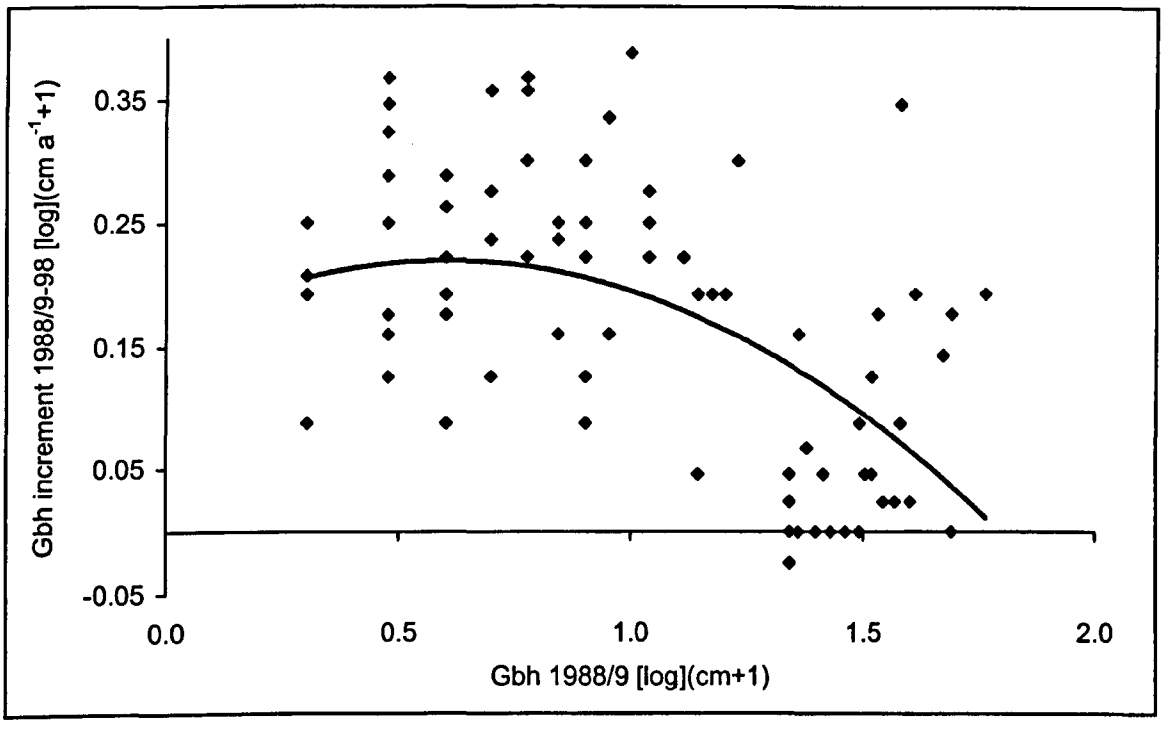
sustained by further windstorm damage during 1988-1992. Most of the seedlings remained in 1998, but were non-vigorous with only 16 having grown to 50-70cm, 13 of which were browsed by deer. Similarly a dense cohort of ash seedlings had established in plot 85 below a medium-sized gap created during 1988-98: again most were non-vigorous, all were browsed by deer, and only ten had grown to 50-80cm tall.

3.2.2.1.4.5. Holly

Mortality of holly in the circular plots over 1987-98 was exceptionally low, with only one of 136 individuals and 11 of 149 stems dying. Accordingly, it had the lowest mortality rate amongst the main species (Table 3.2.6). Middle-sized stems had the highest mortality rates (Table 3.2.9), with seven of the 11 that died being 22-43cm gbh. All seven larger stems survived. Falling trees or boughs struck and crushed/broke most that died, but deer appeared to have killed one, 43cm gbh stem by debarking (even though very little of this was recorded on live stems in 1998). Although relatively few of the losses were noted as damaged in the 1988/9 recording, it is suspected that more were. Falling trees and boughs brought down by windstorms also damaged a substantial number of surviving holly in 1998: 153 of 508 live stems ≥5cm gbh were described as leaning, arched, bent over, lateral, toppled and/or part-broken because they had or were suspected of having been struck. These included 17 larger, 30-66cm gbh stems. Again, although only 24 were noted as damaged in the 1988/9 recording, it is suspected that more were.

Growth of surviving holly stems was slow: gbh/basal area increments averaged only 0.51cm a^{-1}/1.1cm^2 a^{-1}. Gbh increments tended to be lower for the largest stems and higher amongst small-middle sized stems (Figure 3.2.4), but the basal area increments showed no particularly tendency across the size-range.

Figure 3.2.4: Growth of holly stems in the twelve permanent circular plots in The Mens between 1988/9 and 1998. The relationship between the gbh increment (inc_{gbh}) and initial gbh (ini_{gbh}) of stems is shown. The regression line equation is: $\log(inc_{gbh+1}) = -0.1541.\log(ini_{gbh+1})^2 + 0.1852.\log(ini_{gbh+1}) + 0.1637$, n =83, F = 15.8, P< 0.001, $r^2 = 28.3\%$



Holly recruitment was high: 243 individuals and 370 stems grew to ≥1.3m tall or ≥5cm gbh (Table 3.2.6). In addition, 271 small holly individuals <1.3m tall established, including a few, 1-2m wide patches. A minority of these were from layered branches. In fact, recruitment was higher because in plot 78 a dense, 5x5m holly thicket developed blow the opened canopy, within which separate individuals and those <1.3m tall were not recorded. This plot accounted for the majority of the holly recruitment. Seven of the other plots increased by 12-37 stems each and four recruited only 2-5 new stems. However, plot 75 contained 81 individuals <1.3m tall and five others had 16-30 of these in 1998.

Holly was restricted to the understorey in 1998, where it accounted for 64% of stems ≥5cm gbh (Table 3.2.10). Most retained healthy foliage and almost half were noted as vigorous. Only a few individuals/stems showed signs of deer damage (browsing/debarking), though this was clearly limiting the development of some of the short individuals.

3.2.2.1.4.6. Hawthorn

Hawthorn mortality was moderate: 4 of 83 individuals and 22 of 127 stems died over 1987-98 (Table 3.2.6). Mortality rates were highest for 10-<20cm gbh stems and none over 30cm gbh died (Table 3.2.9). Many stems died after being struck, mainly in the 1987 windstorm, but several appeared to have been excluded. In 1998, 82 of the 192 live stems ≥5cm gbh were described as leaning, arched, bent over, lateral, toppled and/or part-broken because they had or probably had been struck by falling trees and boughs brought down during windstorms. These virtually spanned the whole size-range. Although only a minority were noted as damaged in 1988/9, it is suspected that more were.

Many surviving hawthorn stems grew little over 1988-98, with gbh/basal area increment rates averaging only 0.12cm a^{-1}/0.24cm^2 a^{-1}, and there was no significant relationship between the rates and initial size of stems. Compared to holly, hawthorn increment rates were significantly lower: median = 0.11cm gbh a^{-1} and 0.19cm^2 cm basal area a^{-1} for 58 hawthorn stems v 0.50cm gbh a^{-1} and 0.64cm^2 basal area a^{-1} for 83 holly stems (Mann-Whitney rank tests, U = 2733.5-2877, P<0.001).

Hawthorn had 87 stems grow to ≥5cm gbh and ten individuals recruit. The former included several forks/trunk shoots that developed on existing stems, whilst five of the recruiting individuals developed from branches that were pinned to the ground by windblown trees/ branches and which subsequently layered. In addition, 19 small hawthorn <1.3m tall established. Recruitment/establishment was highest in plot 84 (with 28 new stems, six new individuals and ten <1.3m tall) and plot 85 (with 17 new stems, one new individual and seven <1.3m tall), where most were located below canopy gaps.

All hawthorn were located in the understorey in 1998, where they accounted for 21% of stems ≥5cm gbh (Table 3.2.10). 71 stems were described as vigorous, but 20 others had

poor or dead crowns. Seven individuals <1.3m tall were deer-browsed and 14 taller individuals had the basal sprouts eaten down by deer.

3.2.2.1.4.7. Hazel

Hazel lost five individuals and 20 stems due to a combination of breakage during windstorms (mainly the 1987 storm) and exclusion. Accordingly it had higher mortality rates than holly or hawthorn (Table 3.2.6). Mortality rates were higher for middle-large stems (Table 3.2.9), many of which died after being hit. 21 stems grew to ≥5cm gbh and replaced those that were lost. However, these all developed on existing individuals and no new individuals recruited, nor did any seedlings establish. Only eight hazel stems had reliable gbh measurements so stem growth was not analysed. In 1998 there were 16 hazel individuals with 46 stems ≥5cm gbh all growing in the understorey (Table 3.2.10). Most stems were suppressed and non-vigorous below a closed canopy, but 12 were described as vigorous. Deer appeared to have had debarked nearly half of all stems and possibly prevented basal shoots from developing.

3.2.2.1.4.8. Other species

All field maple individuals and stems survived, but none recruited. The three individuals in plot 85 suffered some damage, probably when they were struck, but were resprouting. This plot contained two sets of field maple sprouts growing off root stubs, which were both deer-browsed. The wild service survived, but grew little and retained only one slender, strongly suppressed fork. Deer debarked and killed the small yew in plot 74, but the other survived as an erect, forked bush with the basal sprouts browsed back. The yew just outside plot 76 survived with five live stems and formed a broad, conical, understorey tree. In addition, a single, short yew seedling managed to establish. The only crab apple died, apparently having been hit and broken at 2m up during the 1987 windstorm. This was not

replaced, but a 50cm tall crab seedling did establish below the gap in plot 78. In addition, an 80cm tall blackthorn seedling established in plot 85, though it was browsed.

3.2.2.1.5. Dead wood during 1987-98

3.2.2.1.5.1. Changes in snags in the circular plots

Changes in snags in the circular plots were confounded because it was not possible to identify snags that were blown or knocked over during the 1987 windstorm. In addition, small snags were probably under-recorded in 1988/9. Nevertheless, the basal area and density of snags appeared to have been low before 1987. Of the snags identified, most were <25cm gbh, though seven beech and oak were 45-113cm gbh.

The density and basal area of snags was increased by the 1987 storm and these remained at similar levels in 1998 (Table 3.2.13). Wind-damaged victims accounted for 13 of the 21 snags present in 1988/9, the remainder being trees that seemed to have been excluded beforehand. The 43 snags in 1998 included 19 that had been excluded and 14 that had wind-damaged. Three beech of 24-68cm gbh were from squirrel debarking. Six of the seven largest were all windstorm-victims (mainly wind-snapped oak). Throughout, oak and beech accounted for most of the snag basal area. Although both increased after 1987, beech basal area had declined by 1998 whereas oak had increased further. Beech, hawthorn, hazel and oak accounted for most of the snag density, and all increased after the 1987 storm. Despite this, the relative size-distribution changed little: snags of <30cm gbh remained most numerous (66-74%), whilst larger snags of 70-<150cm gbh remained at 14-18%.

The turnover of snags was substantial (Table 3.2.14). Of those present in 1988/9 only 21% remained standing in 1998, most of which were assumed to have been snags before the 1987 storm. They included two 45-55cm gbh beech and two 95-133cm gbh oak snags, plus

Table 3.2.13: Change in the basal area, density and relative importance of snags in the twelve permanent circular plots in The Mens from just before the 1987 windstorm struck to 1998. Condition before the 1987 windstorm was reconstructed from records made in 1988/9. Includes all dead standing stems ≥5cm gbh. Relative importance = [% total basal area + % all snags]÷2

	Basal area (m^2 ha^{-1})			Density (n ha^{-1})			Relative importance (%)		
	1987	1988/9	1998	1987	1988/9	1998	1987	1988/9	1998
Oak	0.8	1.1	1.6	11	13	16	37	37	43
Beech	0.2	0.7	0.4	21	24	24	31	31	20
Hazel	<0.1	<0.1	<0.1	11	24	27	10	15	13
Hawthorn	<0.1	<0.1	<0.1	13	24	27	12	14	12
Holly	-	<0.1	<0.1	-	3	13	-	2	7
Crab apple	-	<0.1	-	-	3	-	-	2	-
Ash	-	-	<0.1	-	-	5	-	-	3
Yew	-	-	<0.1	-	-	3	-	-	1
All species	1.0	2.0	2.2	56	90	114	100	100	100

Table 3.2.14: Fate, throughput and recruitment of snags in the twelve permanent circular plots in The Mens from just before the 1987 windstorm struck to 1998. The table shows the number of snags in each category, including all dead standing stems ≥5cm gbh; (a) includes live stems in 1988/9 that had died and collapsed by 1998; (b) includes live ≥5cm gbh stems in 1988/9 that had died and which formed snags in 1998; and (c) includes stems <5cm gbh, <1.3m tall or not present in 1988/9 and which formed snags in 1998. Snags in 1987 were reconstructed based on snags recorded in 1988/9

	Snags in 1987	Snags in 1988/9	Fate of 1988/9 snags by 1998		Throughout 1988/9-98	Recruitment 1988/9-98	
			Still standing	Collapsed	(a)	(b)	(c)
Oak	4	5	2	3	-	4	-
Beech	8	9	2	7	14	7	-
Hawthorn	5	9	2	7	9	6	2
Hazel	4	9	1	8	7	8	1
Holly	-	1	-	1	6	4	1
Crab apple	-	1	-	1	-	-	-
Ash	-	-	-	-	-	2	-
Yew	-	-	-	-	-	1	-
Birch	-	-	-	-	3	-	-
All species	21	34	7	27	39	32	4

two hawthorn and a single hazel. Oak snags persisted better than the other species.

Throughput amounted to 39 of 71 live stems ≥5cm gbh, which died during 1988/9-98 but failed to form snags in 1998. There was little difference in the relative size of stems that did or did not form snags, but all oak, ash and yew and most hazel did, whereas less holly, hawthorn and beech and no birch did. Another 36 snags recruited during the period, most

of which were small, but they included four large, 98-148cm gbh, wind-snapped oak, three of which were snapped after the 1987 storm.

3.2.2.1.5.2. Dead wood levels, dimensions and condition in 1998

The abundance, dimensions and condition of larger snags (≥20cm gbh) and fallen dead logs/branches was assessed in detail in 1998 (Table 3.2.15). The combined volume and length of these was 115m^3 ha^{-1} and 5951m ha^{-1} respectively, most of which was on the ground. Many snags were ≥30cm gbh, ≥7m tall, had limited decay and/or most bark still present. Oak accounted for most the snag volume and, along with beech, most of the snag length, density and largest snags. In addition, a few of holly, ash and hazel snags were recorded. About half the fallen logs/branches were ≥30cm girth at the point of intersection, and the majority were classed as rotten or very rotten and with most bark missing. Compared to snags, they were generally more decayed and retained less bark: 101 out of 173 logs/branches were rotten or very rotten whereas none of the 20 snags were ($\chi^2_{(df=1)}$ = 24.5, P<0.001); and 132 out of 173 logs/branches had less than 50% bark compared to only 4 out of 20 snags ($\chi^2_{(df=1)}$ = 27.3, P<0.001). Beech and oak respectively accounted for around 65% and 30% of the total volume and length of logs/branches, with many of the largest logs being of beech. Whereas most beech logs were well decayed and had little bark, most oak logs were relatively solid.

3.2.2.2. Changes in the canopy gap plots

3.2.2.2.1. Initial condition

The total area covered by the nine canopy gaps recorded in 1988 was 4166m^2. These covered 2.5% and included all the major gaps created by the 1987 windstorm within the study area (Figure 3.2.1). The size, shape, dimensions and orientation of each gap differed (Table 3.2.16, for Gaps E-H see Figures 3.2.25a-d). Most were <500m^2 in area, but two were larger at 925-1090m^2. Four were near-oblong, three were near-circular, one was near-

Table 3.2.15: Quantity and condition of larger snags and fallen dead logs/branches as recorded in The Mens in 1998. Snags were measured in the twelve permanent circular plots, whilst fallen logs/branches were measured using line transects throughout surrounding compartment. Cells show the number of snags/logs in each category unless stated otherwise

(a) Snags – based on measurements of snags ≥20cm gbh

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Height			Gbh			Decay state		Remaining bark	
				0-2.5m	3-7m	>7m	20-<30cm	30-<60cm	60-142cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Oak	22.0	212	16	-	-	6	-	-	6	6	-	-	6
Beech	4.9	212	21	1	3	4	2	4	2	8	-	3	5
Holly	0.4	45	8	-	3	-	2	1	-	3	-	-	3
Ash	0.3	42	5	-	1	1	1	1	-	2	-	-	2
Hazel	<0.1	4	3	1	-	-	1	-	-	1	-	1	-
All species	27.7	516	53	2	7	11	6	6	8	20	-	4	16

(b) Fallen logs/branches – based on measurements of dead stems ≥15cm gbh at point of intersection

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Girth at point of intersection			Decay state		Remaining bark	
			15-<30cm	30-<60cm	60-167cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Beech	57.3	3456	57	35	18	35	75	88	12
Oak	27.9	1634	26	17	9	31	21	39	13
Ash	1.0	94	-	3	-	1	2	3	-
Holly	0.7	157	4	1	-	3	2	1	4
Hazel	0.4	31	-	1	-	-	1	-	1
Hawthorn	0.2	31	1	-	-	1	-	-	1
Yew	<0.1	31	1	-	-	1	-	1	-
All species	87.6	5435	89	57	27	72	101	132	41

Table 3.2.16: General characteristics of nine canopy gaps in The Mens created by the 1987 storm and recorded in 1988. For Gaps E-H see Figures 3.2.25a-d

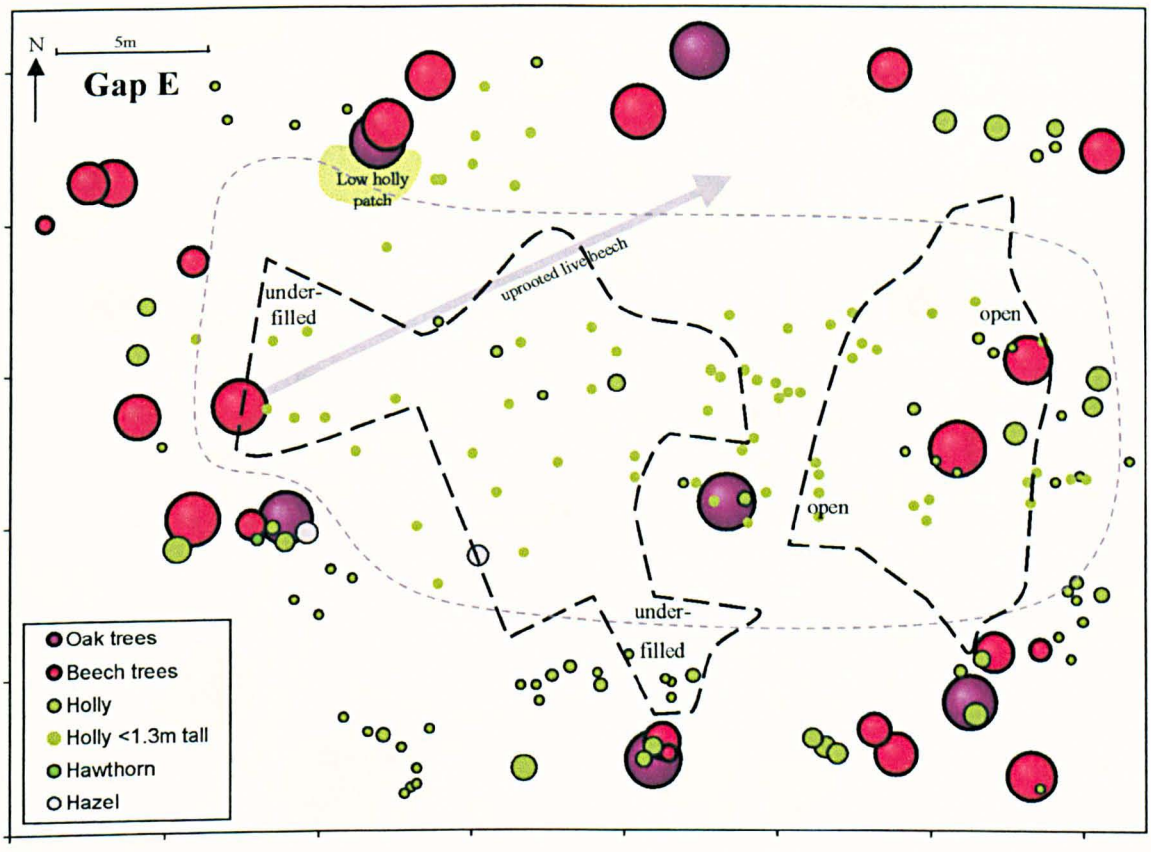
Gap	Area (m^2)	Dimensions, shape and orientation
A	115	12 x 14m near-triangular gap with longest axis bearing approximately ENE-WSW
B	210	11 x 24m near-elliptical gap with longest axis bearing approximately ENE-WSW
C	260	12 x 21m near-rectangular gap with longest axis bearing approximately ENE-WSW
D	305	15-21m diameter near-circular gap
E	360	12 x 31m near-rectangular gap with longest axis bearing approximately E-W
F	410	20-24m diameter near-circular gap
G	490	22 x 29m quasi-rectangular shape with longest axis bearing approximately NNE-SSW
H	925	40m diameter quasi-circular gap with longest axis bearing approximately NNE-SSW
I	1090	20 x 50m near-rectangular gap with longest axis bearing approximately ENE-WSW

triangular, and the other was near-elliptical. Most were <1.5 times longer than wide, but three were 2.2-2.6 times longer than wide. Most had their longest axis heading towards NNE-E (which generally corresponded with the direction the gap marker fell).

A total of 112 trees were involved in the creation of the canopy gap plots (Table 3.2.17), including five trees in plot 78 that were certainly uprooted or broken in the 1987 storm and were adjacent to but not recorded as part of Gap H. Various types and degrees of damage were recorded for each tree: 55 beech, 28 oak and two yew were completely uprooted/broken/crushed; six beech and two oak suffered major crown breakage; and seven beech and twelve oak suffered minor crown breakage. Thus, trees with major damage included relatively more beech (61 of 68 trees) than oak (30 of 42 trees) ($\chi^2 = 6.1$, $P<0.025$). However, c.90% of the oak and only c.40% of the beech were ≥90cm gbh. These trees included 27 beech and 22 oak that were adjudged to have been directly uprooted/ broken by the storm, of which relatively more beech (13 trees) had been uprooted and more oak had been trunk/crown-snapped (20 trees, mainly at 6-12m up the trunk) ($\chi^2 = 8.7$, $P<0.005$). This left 42 trees that were had been indirectly uprooted/broken/crushed, i.e. as other trees fell onto them. Overall, relatively more beech (34 of 61 trees) than oak (8 of 30 trees) ($\chi^2 = 6.8$, $P<0.01$) had major damage.

Figures 3.2.5a-d: Plan view of the detailed recordings of Gaps E, F, G and H in The Mens in 1998. The margins of the gaps are shown for 1988 (light dash) and 1998 (heavy dash), with areas substantially under-filled by beech/oak in 1998 indicated. The symbols represent trees and shrubs present in 1998. Trees present before gap formation are shown separately from trees that recruited (grew to ≥1.3m tall by 1998) and from tree seedlings (which were 40-<130cm tall in 1998). Shrubs were ≥1.3m tall in 1998, unless stated otherwise. In (d) the area covered by shrub growth was plotted, not the individual bushes. The approximate size of each individual is shown based on the gbh of the main stem (stems ≤5cm gbh and seedlings are shown as the same size), but this scale is exaggerated compared to the scale shown on the diagrams. Arrows indicate fallen live trees. Patches of dense ground vegetation and other salient features are indicated

Figure 3.2.5a



NB: most of 1998 gap to the left was open, whilst most of the 1998 gap to the right was under-filled by beech

Figure 3.2.5b

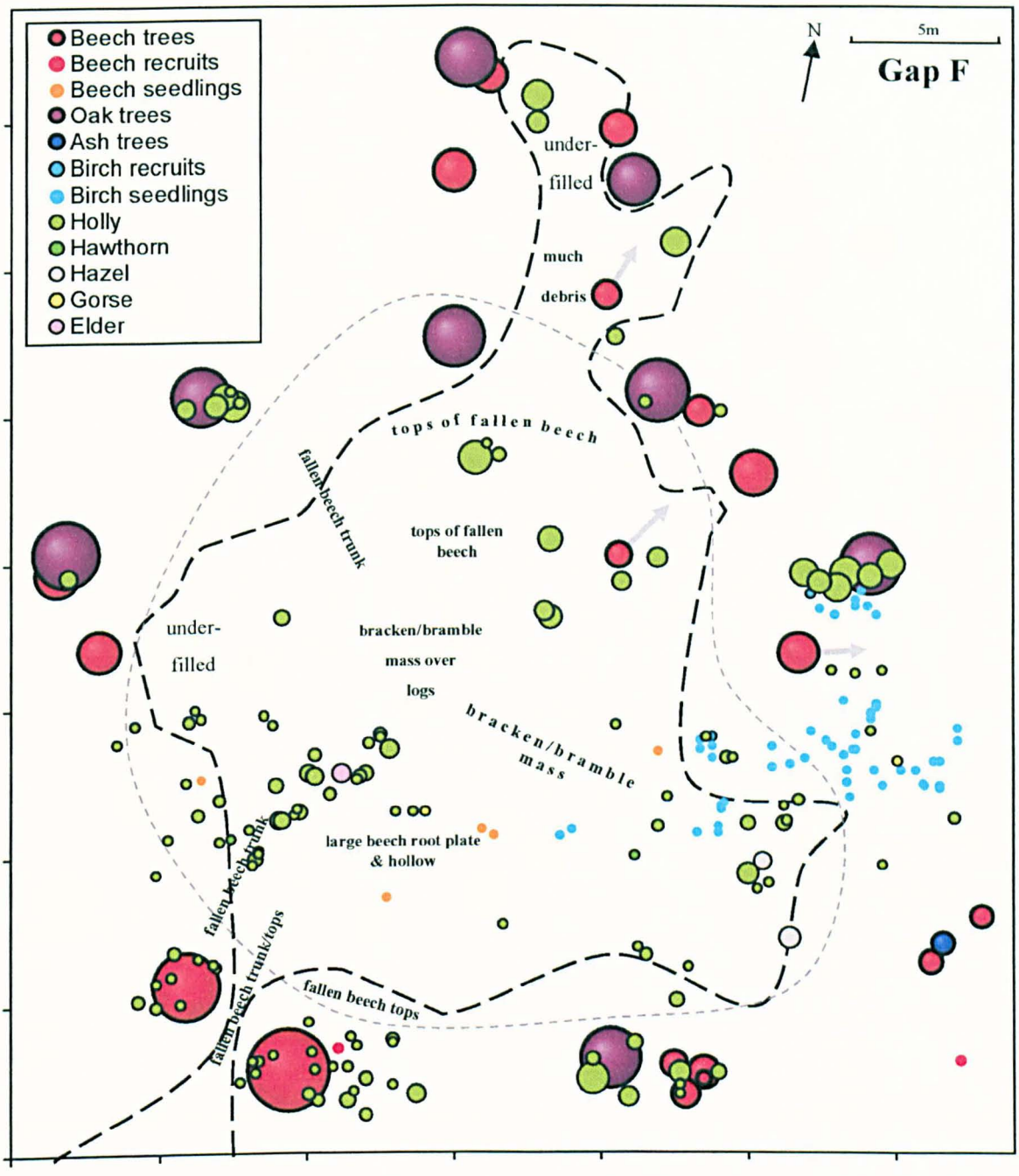

Beech trees
Beech recruits
Beech seedlings
Oak trees
Ash trees
Birch recruits
Birch seedlings
Holly
Hawthorn
Hazel
Gorse
Elder
N
5m
Gap F
under-
filled
much
debris
tops of fallen beech
fallen beech trunk
tops of fallen
beech
under-
filled
bracken/bramble
mass over
logs
bracken/bramble
mass
large beech root plate
& hollow
fallen beech trunk
fallen beech trunk/tops
fallen beech tops

Figure 3.2.5c

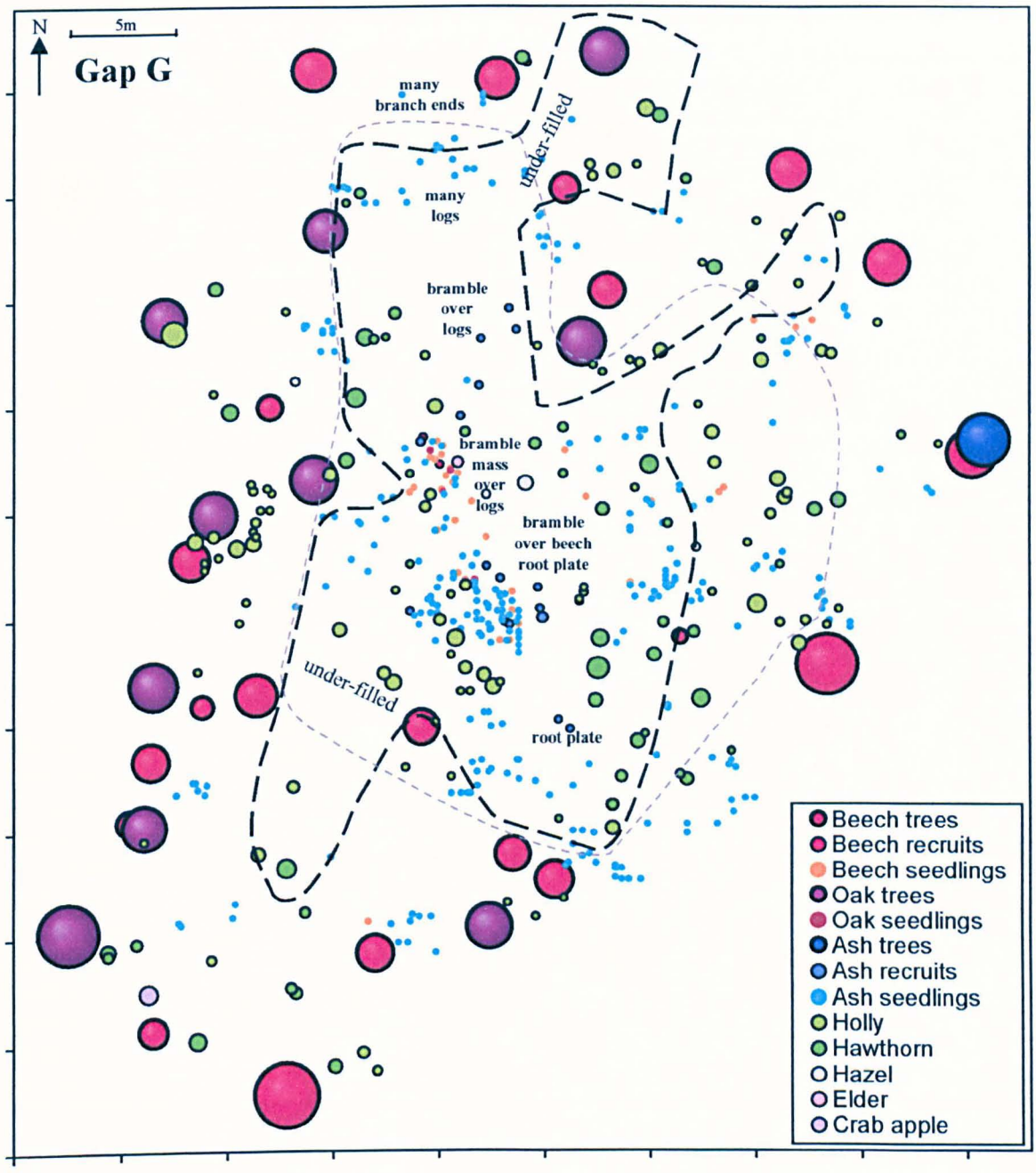
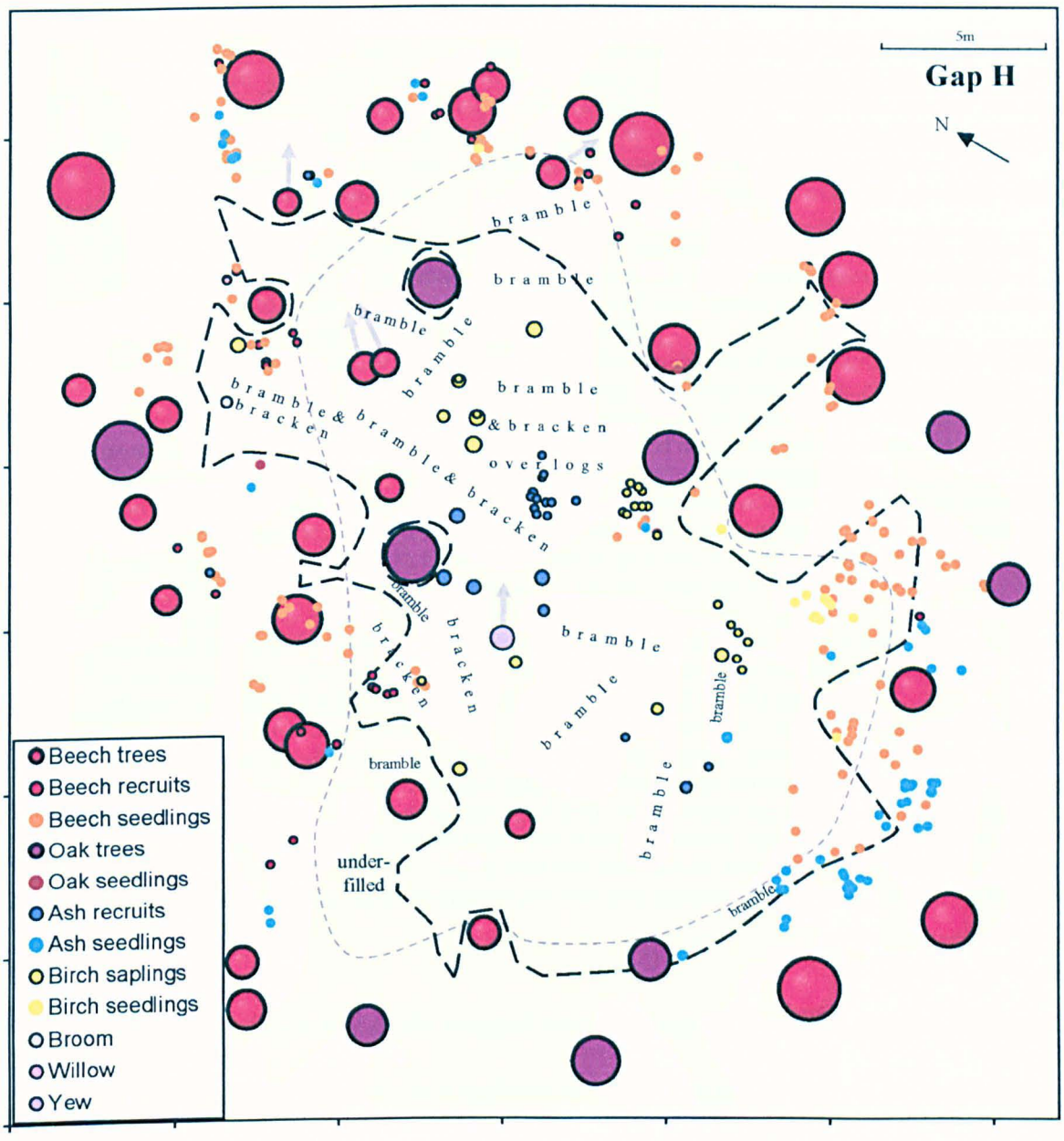

N
5m
Gap G
many branch ends
under-filled
many logs
bramble over logs
bramble mass over logs
bramble over beech root plate
under-filled
root plate
Beech trees
Beech recruits
Beech seedlings
Oak trees
Oak seedlings
Ash trees
Ash recruits
Ash seedlings
Holly
Hawthorn
Hazel
Elder
Crab apple

Figure 3.2.5d



NB: dense shrub growth covered the areas highlighted in green, most of which was holly with a few patches of hawthorn, hazel and yew

Table 3.2.17: Cause of gap formation for nine canopy gaps in The Mens created by the 1987 storm and recorded in 1988. For Gaps E-H see Figures 3.2.25a-d

Gap	Cause of gap formation
A	Basal-snapping of a large beech; trunk snapping on an oak 12m up; major branch breakage on a large marginal beech; and minor branch breakage on a marginal oak – both trunks fell towards NNE-NE
B	Trunk snapping on two oak at 8-12m up and two beech at 10-15m up, which then crushed two smaller beech; and crown branch breakage on two marginal oak – the large snapped trees fell towards E-NE
C	Trunk snapping of a large twin-stemmed beech (one trunk at 7m up and other at ground level); uprooting of a smaller beech; and crown branch breakage on a marginal oak – the beech fell within NE-ENE
D	Uprooting of three beech (one was large and probably knocked over the others and then snapped another two smaller beech); snapping of an oak trunk at 8m, which then snapped a beech below; breakage of a major fork from a beech; and breakage of some crown branches on a marginal oak – the snapped large beech and oak both fell towards NNE-ENE
E	Uprooting of a beech towards ENE, which then broke boughs out of some marginal beech; tipping of another beech; and snapping of two oak (at 6-12m up) and a twin-stemmed beech (at 8-10m up)
F	Uprooting of a large spreading beech to the north, which then brought down six smaller trees (four beech and two oak) and broke some boughs off a marginal oak; breakage of a main fork on a large marginal beech pollard; and breakage of some crown forks on two marginal oak
G	Uprooting of two large beech, which appeared to have then crushed/broke three smaller beech, four oak and some branches on other marginal beech and oak; trunk snapping of an oak; and breakage of 25% of the crown on a large marginal beech, which appeared to have then crushed a smaller beech and broke 30% of the crown out of a marginal oak – the two main uprooted beech almost directly north
H	Breakage of all four large boughs from a large beech pollard, which appeared to have then uprooted one small beech and yew; trunk snapping of eight oak, several of which were apparently then involved in snapping/crushing/uprooting eight other beech – the boughs from the beech pollard and snapped/uprooted trees fell towards N(x3), NNE(x2), NE(x5), E(x1) and SSE(x1)
I	Uprooting of a large beech, which appeared to have then broke 50% of the crown in an oak, snapped two smaller beech and another oak, and crushed a beech sapling; uprooting of a large oak, which appeared to have then snapped a smaller oak, broke 50% of the crown in another large oak, and knocked over two smaller beech; uprooting of three beech, which appeared to have then snapped another beech and broke 60% of the crown out of another beech; trunk-breakage on two beech and three oak, the latter having then knocked over two more beech; breakage of 30-60% of the crown in three other beech; and a large sub-canopy yew was also uprooted – the five uprooted trees fell towards NNE, NE, ENE, NW(x2)

The gaps retained only a few of the original trees/saplings in the lower stratum. These were all beech and included: (i) two intact saplings on north margin of Gap A; (ii) a sub-canopy tree within Gap B; (iii) an unscathed sapling in Gap D; (iv) a sapling and an old stool with three, 2m tall sprouts in Gap G; and (v) a sapling and five sub-canopy trees in Gap I.

3.2.2.2.2. Changes during 1988-98

All gaps had partly filled by 1998 due to crown expansion, epicormic sprout growth on trunks/boughs, and/or low lateral branch/epicormic sprout growth (= sub-canopy under-filling) (Table 3.2.18). Lateral growth of border-trees was mostly around 1-4m. Both beech and oak were important in gap filling, but for beech crown growth (8 gaps) and low lateral

Table 3.2.18: Change in the area covered by nine canopy gaps in The Mens created by the 1987 windstorm and recorded in 1988 and 1998. Note that Gaps B and D became joined. For Gaps E-H see **Figures 3.2.25a-d**

	1988	1988-98			1998
Gap	Area (m^2)	Area of canopy filled (m^2)	Area under-filled (m^2)	Area opened (m^2)	Area (m^2)
A	115	40	0	15	90
C	260	65	0	5	200
B	210	65	0	45	}335
D	305	115	90	45	
E	360	190	79	1	92
F	410	84	16	41	351
G	491	154	44	57	350
H	925	160	40	126	851
I	1090	305	25	25	785
All	4166	1178	294	360	3054

branch growth (five gaps) were important, whereas for oak trunk/crown sprout growth (six gaps) was more important than crown growth (three gaps) (Table 3.2.19). The area filled ranged from 40-330m^2 and generally increased as initial gap size rose (Table 3.2.18). In two gaps (D and E) beech under-filling was particularly important.

By 1998 six gaps had sizeable, newly opened areas along the gap margins. This was related to the windthrow of three beech and one oak, wind-snap of another oak, partial crown snapping in four other oak, and partial crown snapping following squirrel debarking in five beech (Table 3.2.19). Not only did this reduce the area filled by gaps, typically by 10-15%, it also meant that Gaps B and D had become joined by 1998.

Of the 92 storm-damaged oak and beech trees that were uprooted, trunk snapped or had >50% crown snapped out in 1987, 35 survived. These included a similar proportion of uprooted (14 of 39) and trunk/crown-snapped (21 of 53) trees. The proportion of oak and beech that survived was similar (10 of 30 oak, 25 of 62 beech), as was the proportion of oak and beech that survived trunk/crown-snapping (9 of 23 oak, 12 of 30 beech). However, only one of seven oak survived uprooting, whereas 13 of 32 beech did. Most of the unscathed beech saplings survived, but the old beech stool in Gap G died.

Table 3.2.19: Causes of change in the area covered by nine canopy gaps in The Mens created by the 1987 windstorm and recorded in 1998. For Gaps E-H see Figures 3.2.25a-d

Gap	Causes of change in gap area by 1998
A	Closure mostly due to beech crown expansion of up to 3.5m along southern edge and up to 1.9m in north-west corner; oak crowns along the northern edge have hardly expanded at all but vigorous epicormic oak sprouts have grown well – a small new gap area has opened up to west following snapping of a large beech at 1.5m up, apparently not long after 1987 storm, but this is rapidly filling with vigorous beech crown growth
B	Closure mostly due to marginal crown growth, with oak crowns having expanded by up to 1.6m along north side and 3.5m along east side, and beech crowns having expanded by up to 1m along south side; internal filling limited, but surviving snapped beech and oak have sprouted up trunks – gap has expanded to west (and become linked to gap D) where a beech has been windblown (bringing down/snapping other beech in its path) and an oak has lost a large crown branch which was part-snapped in 1987 storm, and to the south-west where another beech has been wind-snapped
C	Closure mostly due to marginal crown growth on beech of up to 3m on north-west side, 2m on south side, and 1m on south-west side; small area filled by sprout growth on a part damaged oak – small new area has opened up along north-east side due to deterioration of upper crown on marginal beech
D	Canopy closure mainly due to vigorous sprout growth on oak plus limited crown expansion on oak and beech filling a sizeable area in the northern half of gap; along south-east edge, vigorous sprout growth on beech and crown expansion on oak and beech of up to 2m has filled only small area; in remaining open area to south-west, sub-canopy beech has under-filled sizeable part of gap, coming from several medium/small trees that have lost their tops due to squirrel debarking and/or storm-breakage – original gap expanded to east and become linked to gap B (see above)
E	Canopy closure due to vigorous growth of both oak and beech; marginal beech has tended to expand more through lateral crown/trunk bough growth, whereas oak has significant trunk sprout growth on several trees; some internal filling has developed from both snapped oak and beech and tipped beech which have vigorous sprout growth – some post-1987 storm damage has occurred along southern margin, where a marginal oak has lost its main central fork and another has had a main fork and other boughs snapped out (but has sprouted vigorously); however this area has mostly been under-filled by beech
F	Canopy closure has occurred along most edges, but is greatest at 4m along west side; majority of filling due to moderate crown expansion on marginal oak and beech, and sprout growth on marginal oak and on large part-snapped marginal beech; only small area has filled with lower lateral growth on marginal beech – gap has expanded to north due to snapping of major fork from a marginal oak, over half of which has been under-filled by low lateral growth on marginal sub-canopy beech and trunk sprouts growth on some marginal oak
G	Canopy closure due to crown expansion on large marginal beech of up to 8m, trunk sprout growth on two marginal oak, and lateral under-filling on several small marginal beech – some edges have opened following windblow of a small beech and an oak, trunk snapping of another oak, and partial crown breakage in two more oak
H	Infilling mainly due to crown expansion, spreading of lower laterals, and trunk sprout growth on several marginal beech; 3 of 8 snapped oak trunks have survived and grown vigorous trunk sprouts – newly opened area has been created by major crown snapping in three marginal beech and an oak, and minor crown snapping in another oak and five beech, with squirrels having induced snapping in two of the latter
I	Canopy closure mainly due to crown expansion and trunk sprout growth on marginal and surviving internal oak along east, south-east, west and south-west sides; marginal and internal beech have expanded vigorously in places, mainly from combination of crown and lateral branch growth, the latter under-filling the gap and coming mainly from medium-sized released beech, most of which have poor, snapped and/or dead crowns due to severe debarking by squirrels – a small newly opened area has been created where a previously undamaged beech to the south has been snapped

Grey squirrels had debarked many of surviving beech around or within the gaps. Only two of five surviving unscathed beech saplings survived without severe debarking, and four beech stems of 24-89cm gbh had died consequently. Of the surviving beech recorded in detail in Gaps E-H, 72% had been debarked by squirrels (Table 3.2.20). The worst damage

was associated with stems sized 20-<120cm gbh, and particularly stems that had been released and had enhanced crown and/or epicormic sprout growth (only 1 of 10 stems with no signs of release were severely damaged or ringed, whereas half of the 48 that were released were this badly damaged; $\chi^2 = 5.4$, $P<0.025$).

Table 3.2.20: Severity of grey squirrel bark-stripping damage to live beech stems as recorded in 1998 in Gaps E, F, G and H in The Mens created by the 1987 windstorm. The number of stems in each category is shown. Stems of 20-<120cm gbh had the highest frequency with moderate or worse damage (46 of 72 compared to 6 of 45 stems in the other size-classes; $\chi^2 = 28.7$, $P<0.001$).

Stem gbh (cm)	Bark-stripping category				
	None	Limited	Moderate	Severe	Very severe
5-<20	18	1	-	-	-
20-<40	2	3	-	1	3
40-<60	-	4	2	6	6
60-<80	1	5	3	4	2
80-<100	-	6	7	4	2
100-<120	1	4	4	2	-
120-<140	-	6	-	2	-
140-310	11	3	4	-	-
Total	33	32	20	19	13

Tree recruitment and seedling establishment within the gaps was patchy and most often poor, though only one had no new recruits or established seedlings (Table 3.2.21). Gap F had a moderate density of established seedlings (Figure 3.2.25b), whilst Gap C had moderate recruitment (346 ha^{-1} based on the original gap area) and Gap G had moderate recruitment (367 ha^{-1}) and a high density of established seedlings (Figure 3.2.25c). However, only Gap H had considerable recruitment (1038 ha^{-1}) and a moderate density of established seedlings (Figure 3.2.25d).

Birch recruited in four gaps (B, D, F, H) and had seedlings establish in three of these (D, F, H) (Table 3.2.21, for Gaps E-H see Figures 3.2.25a-d). The recruits were located mainly in gap centres, on ground that was not shaded initially by shrub growth, and frequently were associated with bramble/bracken. Birch recruitment was most successful in Gap H (Figure 3.2.25d), where 12 of 30 saplings present had grown to 6-8m tall and all looked likely of

Table 3.2.21: Recruitment of trees (≥1.3m in height) and tree seedlings (0.3-<1.3m in height) in nine canopy gaps in The Mens created by the 1987 windstorm and recorded in 1998. For Gaps E-H see **Figures 3.2.25a-d**

Gap	Tree recruitment and seedling establishment
A	No trees recruited – three beech seedlings established, grew to 70cm height, and were located around the northern edge of gap (two looked capable of sustained growth) – a scatter of browsed ash seedlings established, grew to 60cm height, and were located through the gap centre
B	Two birch recruited, grew to 1.5m height, and were located in the gap centre and on the northern edge of a bramble patch that had grown over several large fallen logs; one beech seedling established, located just south of the original gap edge – in the newly-created gap area, a scatter of browsed advanced regeneration ash grew amongst a patch of honeysuckle in the north-central part, but only one had grown to 90cm height
C	Five beech, three ash and a service recruited: in the NW corner of the gap, where there was much holly, three vigorous beech grew to 4m height, a wild service stem grew to 5m, and a spindly ash grew to 3m; across the northern-half of the gap, where holly was sparse, two beech and two ash grew to 2-3m tall – no tree seedlings established
D	One vigorous birch recruited, located in the gap centre and growing out of a small bramble patch – eight birch and three beech seedlings established, all growing through or on the margins of bramble, bracken and/or honeysuckle cover; the birch were mainly located towards the gap centre, whereas the beech were located at the north end of the gap – (details for newly opened area are described under Gap B)
E	No trees recruited – no tree seedlings established
F	Two birch recruited in the eastern quarter of the gap – one beech recruited from a root nodule below a large part-snapped beech, just beyond the south edge of the gap – 50 birch seedlings established, ranging from 40-100cm height, and located around the birch recruits – five beech seedlings established, two in the gap centre on the upturned root plate of the large windblown beech, and with the tallest at 1.1m height in the east quarter of the gap
G	16 ash recruited, grew to 4m height, occurred mostly either in the gap centre or slightly north or east of this, appeared to be from advance regeneration, and were generally protected by a mass of fallen trunks overgrown by bramble; seven attained 2m, two had been badly and two part-debarked at the base, and another two had honeysuckle or bramble growth suppressing the top growth – two beech recruited close to the ash and grew to 1.3-1.6m height – nearly 300 ash seedlings established in many parts of the gap, the highest concentrations occurring throughout the central area and along the northern, southern and parts of the eastern margin; most were non-vigorous, 30-60cm tall, and browsed by deer – 38 beech seedlings established, most of which were located towards the gap centre and browsed by deer; ten had grown to 1-1.3m height and looked set to recruit in the future – five, browsed oak seedlings established and grew to 40-50cm height
H	34 beech recruited, concentrated along the northern margins of the gap, with many growing at or close to the edge of holly bushes; the largest was 2.4m tall and nine attained 2m – 30 birch recruited, mostly in four small groups, the most vigorous of which was slightly north of the gap centre and in the middle of a large patch of dense bramble and bracken growing over fallen trunks and branches, and the least vigorous of which were in the east of the gap centre and growing up between dense holly bushes; the largest birch saplings attained 8m height and 12 were at least 6m – 32 ash recruited, concentrated in the gap centre and growing through or close to a fallen live yew and some holly bushes; five vigorous saplings had been badly debarked low-down and another eight that had been vigorous were already dead due to such debarking; 13 were either non-vigorous, bent over or leaning, and only four were erect and reasonably vigorous, attained 2m and remained undamaged, including the largest that had grown to 6m height – 147 beech seedlings established along all gap margins except the south-west, most of which were <1m height and some of the smallest were browsed down; 17 that attained 1m height looked set to recruit in the near future – twelve birch seedlings had grown to 70cm tall and surrounded the birch recruits – 78 ash seedlings established, mostly just outside the southern gap edge growing between holly bushes, and were non-vigorous, 30-50cm height and browsed by deer – three oak seedlings established, one having grown to 80cm height
I	Four ash recruited, grew to 3m height, and were located in the west quarter of the gap by surrounded holly growth; basal debarking had killed one of the smallest and the others were all part-browsed – two beech recruited, grew to 1.5-2m height, and were located towards the gap centre surrounded by holly – 22 beech seedlings established, many being browsed-down by deer, and most located along a ditch bank in the gap centre or on/beside one of two lifted root plates towards the north and south ends of the gap centre

making canopy trees in this large, slow-closing gap. In the other three gaps, at least one birch recruit/seedling looked capable of sustained growth, though only Gap F looked like it might stay open for several decades.

Ash recruited in four Gaps (C, G-I), had seedlings establish in two of these (G-H) and two others (A, newly opened area in B/D) (Table 3.2.22, for Gaps E-H see Figures 3.2.25a-d). Ash recruits were located mainly around gap centres and not much south of this. At least some appeared to be from advance regeneration or equivalent slow-grown seedlings. All grew in protected locations either encircled by holly bushes or amongst bramble and/or piles of fallen trunks/branches. Basal debarking had severely damaged five and killed eight recruits in Gap H, and killed one recruit in Gap I: the debarking was of some age, but appeared to have been done by bank voles. Ash seedlings were only moderately conservative in their distribution, but the tallest showed a similar preference as birch for central gap areas and protected sites. Most were short, non-vigorous, browsed by deer, and could be classified as newly formed advance regeneration. Although ash recruitment and seedling establishment was abundant in Gaps G and H (Figures 3.2.25c-d), only a few looked capable of sustained growth despite the slow closure of these gaps: erect non-debarked saplings that attained 2m height amounted to only seven in Gap G and four in Gap H. At least one ash recruit looked capable of sustained growth in Gaps C and I, and these were both expected to remain open for several decades.

Beech recruited in five gaps (C, F-I) and had seedlings establish in four of these (F-I) and three others (A, B, D) (Table 3.2.21, for Gaps E-H see Figures 3.2.25a-d). The recruits were located mainly around the centre or towards/along the northern edges of gaps. Many had grown up in protected sites in holly scrub or between fallen logs. Few were greatly affected by deer browsing. Many of the seedlings were also located around or slightly north of the gap centre, but in Gap H (where they were most numerous) they occurred

moreover at the edges and on all sides except the south-west (Figure 3.2.25d). Most were short with only 28 (one in Gap F, ten in Gap G, 17 in Gap H) having grown to 1m in height. Although some were growing in protected sites, notably on the edges of holly bushes, others were more exposed. Deer browsing strongly affected 12 of 38 beech seedlings in Gap G and 29 of 147 in Gap H. Based on appearance, many seedlings looked capable of sustained slow-growth. The best recruitment and seedling establishment was in Gaps H and G (Figures 3.2.25c-d), where 51 and 12 saplings respectively appeared capable of sustained growth in these slowly closing gaps. In addition, Gap C had five such saplings and gap closure was expected to take several decades.

Oak failed to recruit and only eight seedlings established in Gaps G and H. Many were browsed and all were non-vigorous (Table 3.2.21).

Shrub growth was abundant in six gaps (Table 3.2.22, for Gaps E-H see Figures 3.2.25a-d). Virtually all shrubs present before the gaps opened appeared to have survived and been invigorated. In particular, holly had developed, regrown and regenerated strongly to form dense thickets in parts of many gaps and throughout others. Some hawthorn and hazel individuals had also developed/regrown strongly, but recruitment was far more limited. A few broom, elder, gorse and (goat) willow recruited in the centre of some gaps. Deer strongly inhibited holly recruitment in Gap E, where numerous browsed bushes failed to grow up (Figure 3.2.25a). Deer also stopped one crushed hazel from regrowing in Gap E.

In most gaps, some ground vegetation developed in areas that were well-lit areas and not covered by dense holly growth (for gaps E-H see Figures 3.2.25a-d). In particular: a large dense patch of bramble and bracken developed in Gap H; some bramble developed in parts of Gaps A-D, F-G and I; some honeysuckle developed in parts of Gaps A, D, and I; and some bracken developed in parts of Gaps D and F.

Table 3.2.22: Shrub growth in nine canopy gaps in The Mens created by the 1987 windstorm and recorded in 1998. For Gaps E-H see Figure 3.2.25a-d

Gap	Shrub growth
A	Holly has developed, mostly from existing small bushes or as regrowth from struck stems; several substantial linear holly clumps are now present in the gap centre and around the bases of oak to the east – hawthorn has developed vigorously from existing stools and recruited a few saplings
B	Shrubs have made a few gains, with holly having increased, old hawthorn stools/stems around the gap margins having sprouted vigorously, and a few hawthorn seedlings having developed strongly
C	Much of gap has become filled with holly growth: initially, holly was up to 2.5m tall and covered 60-70% of the ground, but has spread vigorously, much has grown to 3-4m height, and only the northern edge of gap lacks abundant holly – two large elders have recruited in the gap centre beside the base of a large snapped beech; each has 2-3 vigorous, 10-25cm gbh, 5-6m tall stems – a few surviving hawthorn are vigorous, and a few hawthorn and hazel have recruited on the northern edge where holly has remained sparse
D	Much of gap has filled with dense holly thickets, with surviving bushes having grown vigorously – a few vigorous hawthorns have survived amongst the holly – one 5cm gbh broom has recruited
E	Holly has become abundant, and includes a few large standing survivors, a very few crushed and re-sprouted individuals, and a few recruits; however most are low-growing bushes that are browsed down by deer – two hazels, which had been hit and laid horizontal by canopy debris, have survived, but the stool within the gap has numerous basal sprouts all browsed down by deer
F	Holly has become abundant along the gap margins, around the bases of the large trees, and in parts of gap centre; although a few, large, multi-stemmed holly bushes survive, most holly are small recruits, the best recruitment having occurred in the west part of the gap; holly crushed by fallen trunks and/or crown debris have invariably developed erect basal or trunk sprouts – two surviving hazels near the south-east corner have been released into vigorous growth, but on one of these two stems have been severely debarked by squirrels and two part-debarked; one hazel seedling has established, but is browsed down by deer – no hawthorn have survived, but two 2-2.5m tall seedlings have recruited, and three 1m tall seedlings have established, one on top of the upturned root plate – one vigorous elder has recruited in the gap centre and grown to 18.5cm gbh – two gorse have recruited, one on top of the root plate and one amongst birch seedlings
G	Some surviving holly and hawthorn bushes have been released into vigorous growth, including a few crushed by debris; both have also recruited a few new individuals – three vigorously re-sprouting hazel occur within the gap, all having been crushed, and two browsed, 80-90cm tall, hazel seedlings have established, and a branch end has layered though the sprouts are browsed down – one released crab apple, one vigorous elder recruit, and a browsed yew seedling are also present
H	Surviving holly and some hawthorn and hazel have been released into vigorous growth, and form dense thickets around most of the gap margins in much of the south part of the gap and across parts of the centre – three, 50-70cm tall, hazel seedlings have established, two of which are browsed – a 3m tall broom recruit, 1.3m long, leaning willow sapling, and a 60cm tall willow seedling are also present
I	Holly has become most abundant, with surviving bushes, including a few crushed individuals and some recruiting stems, having developed strongly to form dense clumps throughout the gap (save for some non-colonised paths and patches between) – a willow sapling in the ditch, a few scattered hawthorn saplings, and a broom sapling just beyond the north edge of the gap are also present

3.3. Stand change and natural disturbance at Toy's Hill

3.3.1. Introduction

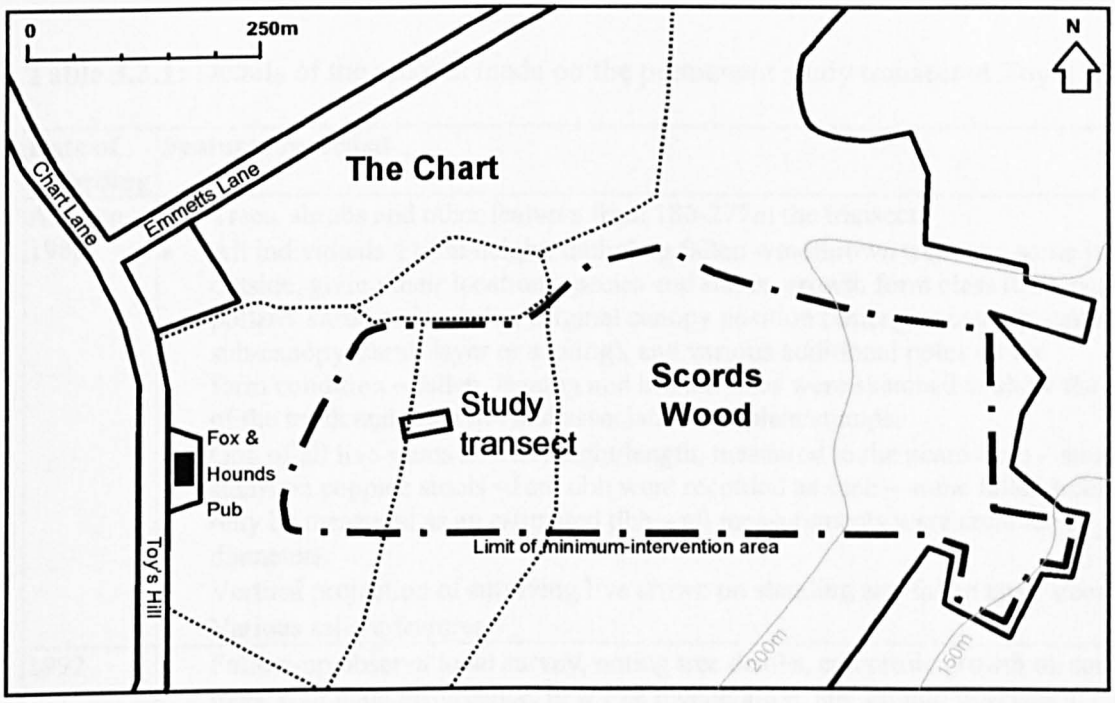
3.3.1.1. Site details

Toy's Hill is located in Kent, south-east England (see Figure 2.1, Table 2.1). It is part of a 154ha Site of Special Scientific Interest, which combines areas of ancient beech-oak woodland and heathland. Much of this is owned and managed by The National Trust, under agreement with English Nature.

The area studied covers about 20ha and forms part of Scords Wood (Figure 3.3.1). It is positioned at about 220-230m above sea level on one of the highest plateaus in the county, and forms part of the Lower Greensand escarpment that crosses north Kent. The underlying soils are moderately acidic, free-draining, typical paleo-argillic brown earths. The most common trees are beech, pedunculate oak and silver birch (see Appendices for scientific names of species). The ground vegetation is locally abundant and dominated by bramble with some stands of bracken. The vegetation appears to conform most closely to the W15 community of the National Vegetation Classification (Rodwell 1991) and stand type 8B of Peterken (1993).

The wood has a long history of human usage (Moseley & Moore 1988, Widdicombe 1996). Traditionally it was an open heathland/wood-pasture with rights for grazing cattle, pannage and firewood collection. In 1853, however, it was enclosed and allowed to develop into dense woodland. Although pollarding of beech and coppicing continued until the 1930s, thereafter it was largely left to develop with minimum intervention. Then, in October 1987 it was badly damaged in a severe windstorm. Much of the old-growth beech-oak stands on the plateau were levelled. Despite many areas being cleared of fallen trees, a central 20ha block in Scords Wood was left untouched and allowed to develop naturally.

Figure 3.3.1: Site map of Scords Wood on the plateau of Toy's Hill, showing the main features, location of the permanent transect studied and area set-aside after the 1987 storm



3.3.1.2. Recording

Details of the aims of recording and methodologies used are given in Section 2.4 and Table 2.3. A single, permanently marked, 20m wide transect was used for recording. This was located across the centre of the minimum-intervention area in Scords Wood on near level ground. A 97m-long section was mapped in detail, which covered 0.194ha. Records were made by Dave Hutton a year after the 1987 storm struck, by Simon Parker in 1992, and most recently in March 1998 (see Table 3.3.1).

3.3.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. The analysis focused on: (i) reconstructing the stand condition just before the 1987 storm struck; (ii) quantifying the impact the storm had on the stand; and (iii) quantifying changes by 1998, particularly in terms of the fate of the original trees, changes to the ground vegetation, and the regeneration that developed. Overall, information was available on

1112 stems/individuals/seedlings/logs. Various standard measures were calculated, and a small number of apparent errors were corrected for.

Table 3.3.1: Details of the records made on the permanent study transect at Toy's Hill

Date of recording	Features recorded
Autumn 1988	• Trees, shrubs and other features from 180-277m the transect. • All individuals ≥1.3m height, including fallen windthrown trees and some just outside, giving their location, species and status, growth form class (tree, coppice, pollard, shrub or juvenile), original canopy position (emergent canopy, canopy, sub-canopy, shrub layer or sapling), and various additional notes on the form/condition – fallen, leaning and broken trees were sketched to show the length of the trunk and branches and associated root plate/stumps. • Gbh of all live stems ≥1.3m height/length, measured to the nearest cm – small stems on coppice stools <1cm dbh were recorded as such – some fallen trees could only be measured as an estimated dbh – all measurements were archived as diameters. • Vertical projection of surviving live crown on standing and fallen large trees. • Various salient features.
1992	• Follow-up observational survey, noting tree deaths, epicormic growth on surviving trees, root plate disturbance, new tree regeneration, and ground vegetation development.
March 1998	From 200-244m on the right-side and from 210-244m on the left-side of the transect: • All individuals ≥1.3m height, giving their location, species and status, including recruits. • Gbh of all live and dead standing stems ≥1.3m height/length, to the nearest half cm. • Detailed notes on the condition of all surviving beech and oak trees and the stature and vigour of recruits. • Snag height and a description of their decay state. • Position of dead fallen windthrown trees, vertical projection of live crowns on standing and fallen trees, and areas covered by dense bramble, bracken and brash. • Various salient features – including location of prominent seedlings and stump regrowth. In addition, from 180-200/210m and from 244-277m, the same records were made for surviving trees, recruits of minor species (i.e. not birch and holly), and the extent dense bramble, bracken, logs or brash.

3.3.2. Results

3.3.2.1. Stand condition before the 1987 storm

The transect sections studied were located in stands that had been treated as wood-pasture up to the mid-1800s, with pollarding continuing to the 1930s. It had then been allowed to infill and developed into dense woodland with numerous outgrown beech pollards. The stand condition just before the 1987 storm was reconstructed using the records made in 1988 (Table 3.3.2), albeit that these probably omitted some small understorey individuals

Table 3.3.2: Reconstructed stand composition in the study area at Toy's Hill immediately before the 1987 storm. Based on records made in September/October 1988 in a 97m-long transect section covering 0.194ha. Stem density and basal area include only live stems ≥1cm dbh

	Beech	Oak	Holly	Rowan	All
Basal area (m^2 ha^{-1})	70.9	4.3	0.2	<0.1	75.4
Stem density (n ha^{-1})	309	16	103	10	438
Density of individuals (n ha^{-1})	186	16	67	5	273
Number individuals recorded	36	3	13	1	53
Number pollards	19	-	-	-	19
Number coppice	13	-	-	-	13
Number self-sown trees	2	1	-	-	3
Number standards	1	2	-	-	3
Number tree from coppice	1	-	-	-	1
Number small shrubs	-	-	13	1	14

that were crushed under toppled trees. The basal area was very high (as there were many large beech pollards), indicative of the old-growth character of the stand. The canopy appeared to have been closed and dominated by outgrown beech pollards. Most of these were single-boled individuals ranging from 59-120cm dbh. The two smallest pollard trunks at 33-42cm dbh were additional boles on a pollard promoted from a coppice stool. The bollings were typically 2-3m tall and had 3-6 major secondary trunks, the largest of which ranged from 25-52cm diameter. Most pollards extended 15-25m into the canopy layer. Five other trees were also in the canopy: (i) three ex-standards (a beech at 90cm dbh and two oaks at 50 and 81cm dbh); (ii) a twin-stemmed beech promoted from coppice with the dominant stem at 63cm dbh; and (iii) a slender self-sown oak at 38cm dbh.

Beech was also numerous in the sub-canopy and shrub layer, with 13 coppice and two self-sown beech present in the lower strata. Most of the coppice individuals had 2-3 main stems up to 17cm dbh, whilst the self-sown trees were 12cm dbh. In addition, 13 shrub holly were present. These were scattered along the transect and mostly formed small bushes, though two were somewhat larger with the main stem at 9-10cm dbh. A single shrub rowan was also probably present.

There were a few notable large snags and stumps including: an 80cm dbh beech pollard; a beech stump from a low-cut pollard; a 1.8m tall shell from a large old holly pollard; and two 70cm diameter stumps from a felled oak and a decaying beech or holly stool. Other snags might have been present, but were crushed or covered over by the time the 1988 recording was made.

Thus, prior to the 1987 storm the area could be described as an old-growth stand, dominated by beech with some oak and with some sizeable pieces of deadwood present. The beech understorey and pollards were last cropped many decades ago, save for a few beech and oak standards that were retained. Although some intermediate felling had occurred, probably for safety reasons, development appears to have been relatively natural.

3.3.2.2. Impact of the 1987 storm

The 1987 storm devastated the stand under study (Table 3.3.3). Canopy cover was reduced to just 2%. Only three, well-spaced beech remained upright and retained any upper crown: two smaller pollards at 59cm and 78cm dbh with 2-3 secondary trunks on top and one slender tree. Another small 33cm dbh beech bolling survived with minimal damage, but this was part of what had been a three-trunked pollard individual that had lost the 42cm dbh bolling and the upper forks from the largest 100cm bolling. The other five large individuals that remained standing suffered major crown loss including: (i) four beech pollards that had most secondary trunks snapped off a few metres above the bolling top; and (ii) the largest oak standard that had most upper forks snapped high up. The remaining large trees were toppled by the storm including: 11 beech pollards; two beech trees; the two smaller oak trees; and a 90cm dbh beech pollard that was windsnapped leaving a 1.5m tall shattered snag.

The windthrow produced 14 hinged and one sheared root plate. These were mostly 2-3m

Table 3.3.3: Condition of individuals recorded in the study area at Toy's Hill one year after the 1987 storm. Unless stated, individuals remained alive. Based on records made in September/October 1988 in a 97m-long transect section covering 0.194ha

	Beech pollards	Beech standards & other canopy trees	Beech coppice & small self-sown trees	Oak standards & other canopy trees	Holly	Rowan
Standing with minor crown loss	2	-	1	-	5	-
Standing with major crown loss	5	-	-	1	-	-
Windthrown	11	2	1	2	-	-
Dead windsplit	1	-	-	-	-	-
Hit & stems snapped off	-	-	5	-	2	-
Crushed/bent over/pinned	-	-	5	-	6	1
Dead hit & snapped off	-	-	2	-	-	-
Hit leaning over	-	-	1	-	-	-

height, 3-5m across, and 0.5m deep. The uprooting disturbed 5% of the ground. Direction of fall was recorded for 17 large windthrown trees, including two beech pollards located just outside that fell across the transect. The range of fall was 235-329°, with most 16 found within a 90° arc from WSW to NNW, the median direction being 293°. This indicated that intense gusts blew from ESE during the storm.

Although one five-stemmed coppice beech individual was windthrown without being hit, most lower strata individuals suffered damage because large falling trees hit them. Of the coppice and small-self sown beech individuals: seven had the tops snapped off all or most of the main stems; five others were completely crushed; and one survived leaning over by 40° beneath some windsnapped oaks limbs. Four hollies were bent over and two were pinned by toppled trees. Two other hollies remained standing, but had their tops snapped off. A toppled tree appeared to have crushed the rowan. Only one coppice beech and five shrub hollies had apparently avoided serious damage from falling trees and debris.

Despite the devastating damage and the description of a few fallen crowns as dead/dying in 1988, most standing and toppled trees were alive one year after the storm. Immediate deaths included only one snapped beech coppice, a small self-sown beech, and a split

pollard beech. However, some lower strata individuals that were crushed beneath the fallen trunks/debris and failed to re-sprout could easily have been overlooked.

Fallen crowns covered a major part (23%) of the of the study area, and combined with the abundant fallen trunks and lower branches to shade much of the ground. Nevertheless, several patches of fully-lit ground occurred between the ranks of fallen trees. But only two small bramble recruits were plotted.

New regeneration included: (i) a group of birch seedlings to 40cm height, which occupied a $10m^2$ block; (ii) seven beech seedlings on root mounds or the edges of associated hollows; and (iii) three scattered holly seedlings. Some of these beech and holly were possibly surviving advance regeneration: this appeared to be the case for four groups of small holly seedlings/layers, two sets of basal growth from old pollard holly snags, and seven patches of low layer-type growth found around surviving or bent over hollies. Regenerating individuals that appeared to have been reduced by the storm amounted to: (i) five damaged beech coppice stools with basal regrowth from 50-120cm height; (ii) two sets of beech root with short sprouts that had been left in the ground when the associated pollard was windthrown; and (iii) the crushed rowan. Two oaks showed signs of regrowth, including the large standard oak, which had many epicormics present where the upper branches had been windsnapped, and the windblown 38cm dbh tree, which had 25-30cm long epicormics all up the trunk.

3.3.2.3. Status four years after the 1987 storm

The records made in 1992 were mainly descriptive, but contained some details on tree mortality. Most fallen trees were reported as dead, in an advanced state of decay and with decaying fungi present. In fact, seven of the 14 windthrown beech had died (five pollards and both trees), but the two windthrown beech pollards and the windthrown oak were

erroneously recorded as 'dead' (as they were alive in 1998). Also, the state of decay was exaggerated. In addition, one fallen oak was recorded with epicormic growth.

Regeneration was noted as being widespread. It was especially abundant in open areas, with vigorous growth of birch to 15 individuals per m^2. Holly patches had increased notably in area and height. The ground flora had developed too, with rosebay willowherb and foxglove dominant. Hard fern was apparent around the base of root pits. Some of the lifted root plates had started to deteriorate, with heavy rains blamed for recent erosion.

There had been some disturbance when a foot path that originally crossed the transect was reinstated: a windthrown beech pollard had had its top cut off, and other material, ground vegetation and regeneration had apparently been cut, cleared or moved to the path edge.

3.3.2.4. Status eleven years after the 1987 storm

The reinstated 2m-wide footpath was in regular use in 1998, with any regeneration and dense ground vegetation having been lost. Although only part of the transect was sampled in 1998, the conditions outlined below were repeated in the next and previous sections and generally across the plateau.

3.3.2.4.1. Fate of original trees

The 1998 recording came eleven growing seasons after the 1987 storm struck. By this time many larger trees had died. Within the transect this included: (i) ten of 12 windthrown/ snapped beech pollards; (ii) both larger beech trees and the smaller oak that were windthrown; and (iii) two of five beech pollards that remained standing after the storm but with major crown loss (Table 3.3.4). In addition, two other bollings died off on pollard beech individuals. Including trees recorded outside the transect, only three of 20 uprooted beech trees/bollings remained alive in 1998. Some of the trees that died were located

Table 3.3.4: Condition of individuals recorded in the study area at Toy's Hill eleven years after the 1987 storm. Based on records made in March 1998 in a 97m-long transect section covering 0.194ha

	Beech pollards	Beech standards & other canopy trees	Beech coppice & small self-sown trees	Oak standards & other canopy trees	Holly	Rowan
Dead	12	2	7	1	-	-
Standing with minor crown loss & sprouting	1	-	1[a]	-	5	-
Standing with major crown loss & sprouting	3	-	-	1	-	-
Windthrown & sprouting	2	-	1	1	-	-
Windthrown during 1988-99 & weakly sprouting	1[a]	-	-	-	-	-
Crushed, bent over or pinned & sprouting	-	-	2	-	6	1
Hit & snapped by other trees & sprouting	-	-	2	-	2	-
Hit & snapped by other trees but not sprouting	-	-	2	-	-	-

[a] top was cropped when path was reinstated

beside the reinstated footpath and had been cut with chainsaws: (i) a windthrown beech pollard had its bolling cut through causing the root plate to slumped back; (ii) two standing beech pollards that suffered major crown loss had their remaining secondary trunks cut off; and (iii) the smallest standing bolling on the three-trunked pollard beech had most of the sprouts on the bolling top cut off. With the death of so many large fallen trees, the area covered by fallen live crown decreased to just 6%. The total would have dropped even further, except that a post-1988 windblown beech fell into the transect and remained with a live crown in 1998.

All five surviving large individuals that were left standing after the storm were sprouting. On four of the surviving beech pollards the bolling tops and small broken secondaries had vigorous sprout growth, though one had been badly debarked by squirrels, the other had the lower side branch forks cut off, and the remaining major secondary trunks still had poor crowns and few trunk sprouts. On two of the beech pollards, vigorous basal/root sprouts had developed. In addition, two beech pollards that had reliable dbh measurements

had increased on averaged 0.58-0.65cm dbh per year since 1988. On the standing oak, which had several snapped limbs still hanging, parts of the trunk bark had died and the dbh increment since 1988 was negligible. However, the surviving forks and lower trunk sprouts had shot strongly. Even so, by 1998 total canopy cover had only increased slightly to 3%, with all five standing trees showing marginal increases in canopy area.

The three surviving trees windthrown in 1987 had also sprouted. These included two fallen beech pollards that had new erect vigorous sprouts developing close to the bolling top on smaller secondaries (though on one some of these had been chainsawed off). Even the large secondaries remained alive on these (despite the upper bark sloughing) and some new crown sprouts and spreading laterals were developed. On the surviving, medium-sized windthrown oak, most of the crown had been shattered by the fall, but numerous erect vigorous sprouts had developed along the crown forks and several very vigorous, large sprouts had shot up near the trunk base. A further windthrown beech pollard, which toppled after 1988, had not sprouted: much of upper crown on this had been sided-up along footpath to leave the remaining branches weakly alive with only a few non-vigorous trunk sprouts present.

The beech coppice and small self-sown trees suffered lower mortality than the beech pollards and canopy trees (47% compared to 67% loss). The seven individuals that did die had all been struck. Most surviving individuals had started to sprout by 1998, either at the base or higher up. Only two failed to sprout noticeably and both were single-stemmed trees that had been bent over or snapped at 3-4m up. In addition, all 13 holly individuals present before the storm had developed strongly to form erect vigorous bushes, and a crushed rowan had developed into a vigorous multi-stemmed individual.

3.3.2.4.2. Regeneration

Copious new regeneration had developed by 1998. This was mostly of birch with some holly, with few individuals of other species recorded (Table 3.3.5). In total 701 new birch saplings were mapped. Another 54 birch saplings were already dead, all but two of which had been excluded and were <2cm dbh. All of the new saplings were post-1988 recruits (the seedling group recorded in 1988 was largely destroyed when the footpath was reinstated). Most must have established soon after 1988. The most vigorous had attained increments of around 1cm dbh and 1m height per year. By 1998 they had reached 6-11cm dbh (Figure 3.3.2). Some saplings, across a wide range of sizes, were either bent over or had the central leader damaged or killed off. These appeared to have been struck by branches or trunks that had come out standing trees, snags, or when already windblown trees had resettled. However, some had been badly debarked by squirrels. Although many appeared to have been permanently reduced in vigour, some of larger stems were vigorously re-sprouting and it seemed as if they might recover.

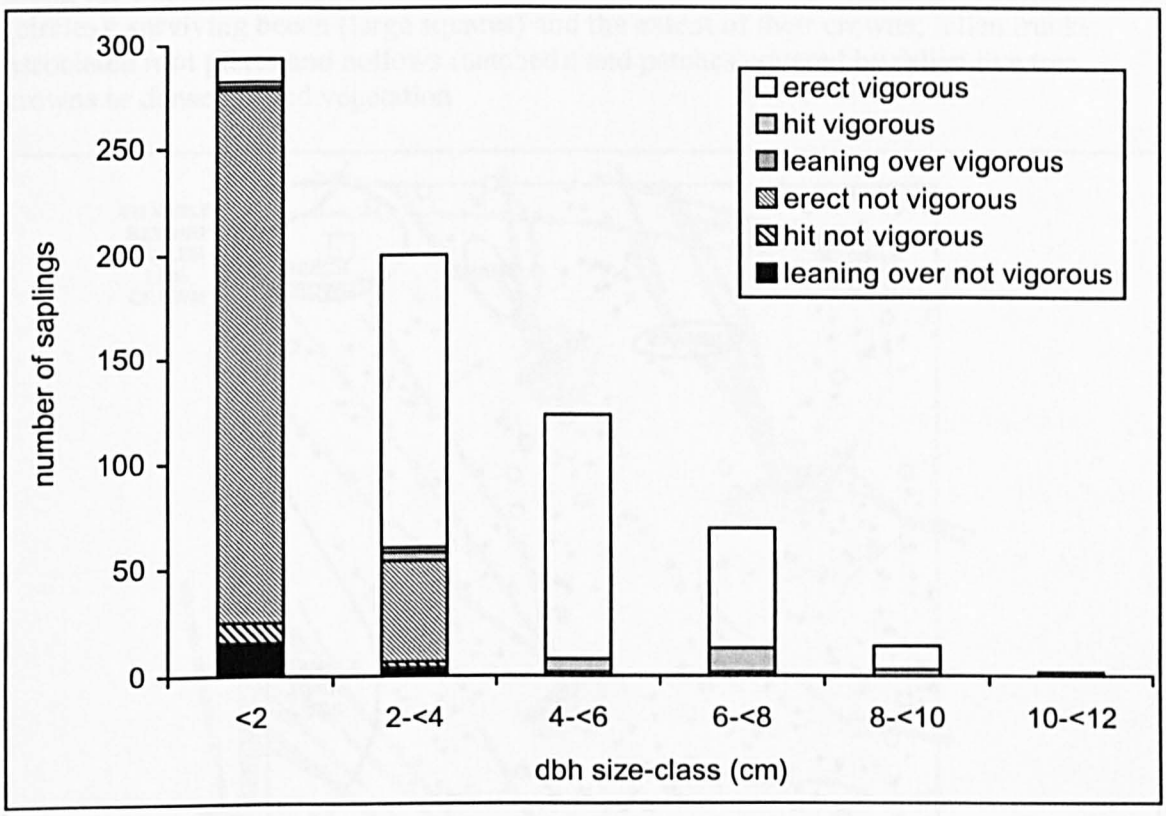
Table 3.3.5: Details of the regeneration recorded in the study area at Toy's Hill eleven years after the 1987 storm. Based on records made in March 1998, with the birch and holly measured in an area of 0.078ha and other species in an area of 0.194ha

	Birch	Holly	Beech	Oak	Rowan	Goat willow	Rhodo-dendron
Recruits alive >1.3m							
Newly established (n)[1]	701	29	3	2	1	1	-
Regrown from sprouts/layers (n)[2]	-	2	13	2	1	-	-
Density of individuals alive >1.3m (n ha^{-1})	8987	397	82	21	10	5	-
Individuals alive <1.3m (n)							
Prominent seedlings	1	1	4	1	2	-	1[3]
Layers	-	1	1	-	-	-	-

[1] recruited since 1987 storm from seed origin except hollies which included many layers and some advance regeneration; [2] from individuals present before and damaged by the 1987 storm; [3] origin unsure.

The birch saplings were noticeably clumped (Figure 3.3.3). Most were in areas that had remained fully-lit. Few occurred on ground covered by fallen trunks, crown debris, fallen live crown or thickets of holly regeneration. Nor were they numerous where patches of bramble or bracken had developed strongly. A few had developed on root plates. The

Figure 3.3.2: Size-class distribution and condition of birch recruits recorded in the study area at Toy's Hill eleven years after the 1987 storm. Based on records made in March 1998

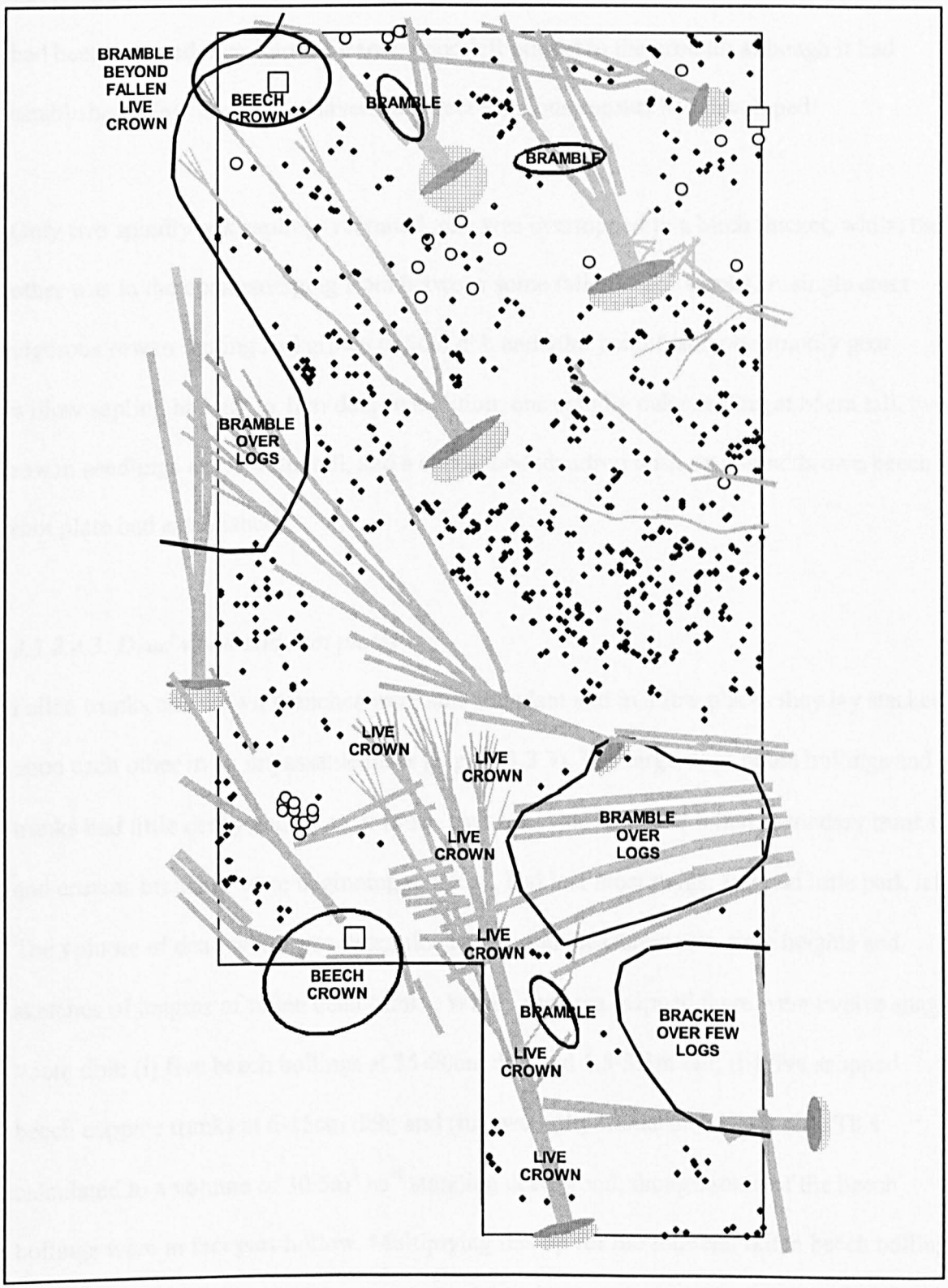


largest diameter saplings were concentrated along the edges of the main groups or were isolated individuals close to the dense bracken area, where inter-specific competition was least and access to light high.

29 holly 'recruits' were recorded. At least seven appeared to have been low-growing specimens before the storm, including two at the base of old holly pollards. Some of the 24 holly recruits with one- to three-stems could have been from seed, but most appeared to be from sucker-type growth from individuals established before the storm. Certainly the other three recruits with 4-8 stems and two with 31-35 stems were dominated by sucker-type growth. Most recruits were erect, vigorous and part of several localised thickets, which could well have been established before the 1987 storm struck (Figure 3.3.3).

Beech had recruited only three new saplings by 1998. Two had grown up after 1988. One

Figure 3.3.3: Distribution of regeneration, surviving and fallen trees, and ground vegetation at Toy's Hill eleven years after the 1987 storm, as recorded from 200-244m along the transect in March 1998. Shown are: recruits of birch (black diamonds) and holly (circles); surviving beech (large squares) and the extent of their crowns; fallen trunks, associated root plates and hollows (hatched); and patches covered by fallen live tree crowns or dense ground vegetation



was a surviving seedling from the seven mapped in 1988. A fourth individual had established where three erect vigorous sprouts had shot up from the root nodules left in the ground from a windthrown pollard. Four new beech seedlings had established by 1998: three were 50-100cm tall; the other was 30cm tall and browsed. In addition, a small beech had been snapped over into the transect and left pinned to the ground: although it had established a few branch end layers, no erect vigorous sprouts had developed.

Only two spindly oak saplings recruited: one was overtopped in a birch thicket, whilst the other was in the open emerging from between some fallen beech trunks. A single erect vigorous rowan sapling had grown to 5cm dbh and 10m height, and one spindly goat willow sapling had got to 1cm dbh. In addition, one spindly oak seedling at 85cm tall, two rowan seedlings at 1.1-1.2m tall, and a small rhododendron bush on a windthrown beech root plate had established.

3.3.2.4.3. Dead wood and root plates

Fallen trunks and crown branches were still abundant and in a few places they lay stacked upon each other in an impassable mass (Figure 3.3.3). The large dead fallen bollings and trunks had little decay and some or much bark left, whereas dead fallen secondary trunks and crowns branches were beginning to decay, had lost most twigs, and had little bark left. The volume of dead wood was determined from dbh measurements, snag heights and sketches of lengths of fallen dead trunks. Within the area mapped there were twelve snags >5cm dbh: (i) five beech bollings at 35-90cm dbh and 1.5-3.5m tall; (ii) five snapped beech coppice trunks at 6-15cm dbh; and (iii) two holly trunks at 6-10cm dbh. This calculated to a volume of 30.5m^3 ha^{-1} standing dead wood, though some of the beech bollings were in fact part-hollow. Multiplying this up for the fourteen fallen beech bollings within the transect area produced about 400m^3 ha^{-1} fallen dead wood volume, which with some additional material in the fallen secondary trunks, created an estimated total of

around 500m^3 ha^{-1}, not an unreasonable value for a collapsed mature beech stand. All root plates were discernable, though many had lost at least some soil. On some much of the associated hollow had been infilled, but a few others remained virtually unchanged.

3.3.2.4.4. Ground vegetation

The ground vegetation had changed considerably since 1992. Instead of willowherb and foxglove, bramble and bracken had become dominant. Several patches of dense sprawling bramble had grown over areas covered mostly by fallen dead crown debris, and in one place dense bracken had developed over an area with few logs (Figure 3.3.3). Although the ground vegetation remained abundant where birch regeneration was lacking, bramble was being shaded out below areas where the birch canopy had closed. Hard fern was still abundant around the hollow of one of the windthrown beech pollards.

3.4. Stand change and natural disturbance at Monks Wood

3.4.1. Introduction

3.4.1.1. Site details

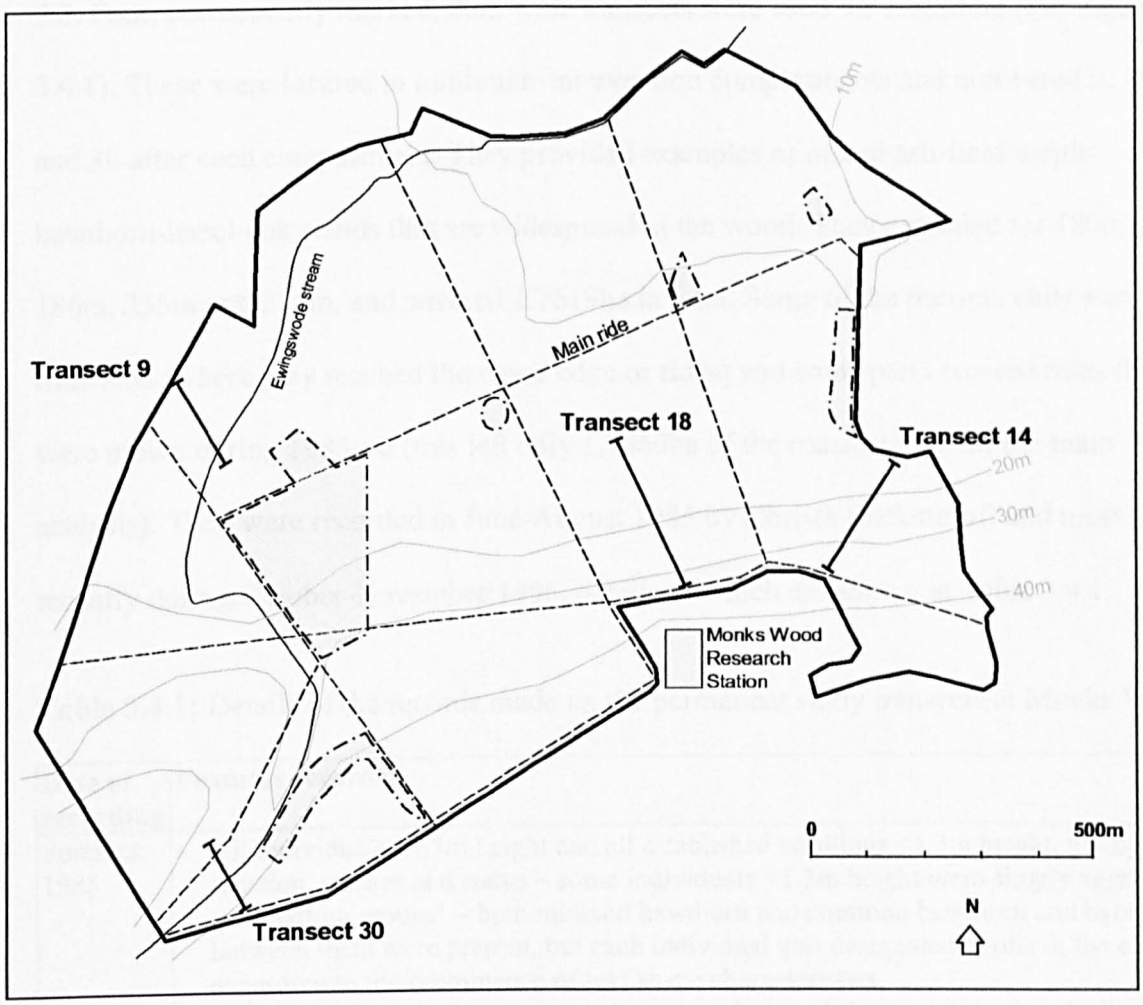
Monks Wood is located in Cambridgeshire, east England (see Figure 2.1, Table 2.1). Steele & Welch (1973) and Massey & Welch (1994) give details of the site. It forms one of the best ancient, semi-natural ash-oak-maple woods on clay in the English lowlands. As early as 1953 it was designated as a National Nature Reserve and remains under the ownership and management of English Nature.

The reserve covers 157ha and descends across moderate slopes from about 40m to 10m above sea level (Figure 3.4.1). The highest, southern part of the reserve lies on the edge of a relatively flat plateau and is underlain by chalky boulder clay that gives rise to moderately well drained, calcareous, clay loams. It then slopes down towards the centre and north, where the ground is near-flat, low-lying and mostly underlain by Oxford clay. Drainage here is poor and the clay soils are mainly calcareous, surface water gleys.

Most of the wood is dominant by ash (see Appendix for scientific names of species), though field maple is widespread and sometimes abundant, and large pedunculate oak trees are scattered throughout. Smooth-leaved elm forms a few dense stands. The understorey is typically well developed and mostly of hazel and common/midland hawthorn. There are many minor woody species present. The ground vegetation on better-drained soils is dominated mainly by dog's mercury and bramble along with a range other plants. The vegetation corresponds mostly to community W8 of the National Vegetation Classification (Rodwell 1991) and stand-type 2Aa of Peterken (1993a).

Although the wood is ancient, some of it occurs on ground that was farmland in historic times (Steele & Welch 1973). Traditionally it was managed as coppice-with-standards

Figure 3.4.1: Monks Wood site map showing the main features of the reserve and the location of the four permanent transects studied. Apart from some coppiced areas (grey shade) and management of rides, most of the reserve is treated as minimum-intervention



with ash and oak as the main trees. Then, during 1914-20, most of the wood was felled leaving only a scatter of trees, and the stands were left to naturally regenerate. Since the 1950s coppice management has been reintroduced to about 13ha and a series of rides reinstated (see Figure 3.4.1). The latter has involved opening up several 10-20m wide rides, which have the central strip mown and the edges rotationally coppiced. The remaining stands (c.135ha) have been retained without any treatment. In recent decades the vegetation of the wood has changed considerably in response to various factors (Massey & Welch 1994, Crampton *et al.* 1998, Cooke & Farrell 2001), including increased browsing by Chinese muntjac deer *Muntiacus reevesi*. This was first sighted in the wood in about 1970 and, after 1985 expanded into an exceptionally large population of about 190 deer. These remained numerous until 1998/9 when a cull began to reduce numbers.

3.4.1.2. Recording

Details of the aims of recording and methodologies used are given in Section 2.4 and Table 2.3. Four, permanently marked, 20m wide transects were used for recording (see Figure 3.4.1). These were located in minimum-intervention compartments and numbered 9, 14, 18 and 30 after each compartment. They provided examples of mixed ash-field maple-hawthorn-hazel-oak stands that are widespread in the wood. They extended for 180m, 186m, 255m and 275m, and covered 1.7619ha in total. Some of the transect ends were truncated (where they reached the wood edge or rides) and some parts crossed rides that were mown during 1985-96 (this left only 1.7060ha of the transect area for the main analysis). They were recorded in June-August 1985 by Christa Backmeroff and most recently during October-November 1996, details of which are shown in Table 3.4.1.

Table 3.4.1: Details of the records made on the permanent study transects at Monks Wood

Date of recording	Features recorded
Summer 1985	• All individuals ≥1.3m height and all established seedlings <1.3m height, giving their location, species and status – some individuals <1.3m height were simply aggregated as 'seedling groups' – both midland hawthorn and common hawthorn and hybrids between them were present, but each individual was designated to one or the other according to the prominence of leaf shape characteristics. • Gbh of all live and dead stems ≥5cm gbh and many below, measured to the nearest cm. • Position of various larger fallen dead logs (criteria not specified), often with a gbh measurement for the largest end and indication of the species. • Various salient features. • Most records were drawn onto a set of A4 scale charts, each covering a 30m long transect section.
Autumn 1996	• All individuals ≥1.3m height and all established seedlings, giving their location and status. • Gbh of all live stems ≥3cm gbh (except for privet that was measured at ground level) and all dead stems ≥5cm gbh, measured to the nearest half cm. • Condition of live stems, including descriptive notes and allocation of crown position, crown size, crown die back, and cause of demise for stems that had been lost. • Snag height and description of decay state, and condition of logs plotted in 1985. • Fallen dead wood abundance and condition – this was done using twenty-seven, 20m long line transects, positioned every 30m across the middle of the transects, and by measuring the girth or diameter (to nearest cm) of all fallen dead stems ≥15cm girth where they crossed the lines and taking notes on their origin and condition – in addition, all fallen dead logs within the transects that were ≥45cm girth at the largest end and ≥2m length were mapped and measured, taking the girth at both ends – the origin and condition of all recorded pieces was noted. • Extent of canopy gaps and notes on their origin and understorey infilling. • Various salient features.

3.4.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. Firstly, the analysis focused on the general changes in stand composition and structure since the last major felling in 1914-1920 and up to 1985 based on an assessment of the stand characteristics when the transects were first recorded. A more detailed analysis of stand changes during 1985-96 was made by comparing the features recorded at both dates and by an assessment of the additional features recorded in 1996. The four transects were combined for these analyses: although there was some variation in the distribution of tree/shrub species, there was no obvious major distinction between them worthy of making any major division. A total of 1.7060ha of the transect area was included in the main analysis, with the main areas directly affected by ride management being excluded.

The data set provided information on 9859 stems/individuals/seedlings/logs. A small number of mistakes and apparent errors were corrected for and various assumptions were made. The main problem was with stem relocation and gbh measurement on complex, multi-stemmed and forked hazels and hawthorns, particularly the latter where sharp, sturdy spines had to be combated. In addition, many additional trunk shoots and side forks that appeared to have been omitted in 1985. Various standard measures were calculated, with annual rates of change being based on 11 growing seasons, and stems <5cm gbh recorded in 1985 being scored as 3cm gbh for basal area calculations.

3.4.2. Results

3.4.2.1. Stand development before 1985

The study transects were located in stands that were virtually cleared felled in 1914-20 and left to naturally regenerate and develop without treatment. However, some sections were adjacent to or dissected by rides, which increased the amount of side-light they received. In 1985 the transects were dominated by dense, high forest stands, with 17 tree and shrub

species represented (Table 3.4.1). They mainly comprised an overstorey of ash and oak, and a sub-canopy/understorey of field maple, hazel and common and midland hawthorn. The basal area was around $28m^2$ ha^{-1}. A scatter of large individuals was recorded (Table 3.4.1): these must have been retained during the 1914-20 fellings. They were mainly standards and stored stools of oak, ash and field maple, plus a single wild service. Perhaps the largest hawthorn bushes and crab apple had also been spared. Although it was difficult to decide exactly which individuals were retained, if all those attaining 120cm gbh were included this gave a density of 28 trees ha^{-1}. Clearly the early 20^{th} century fellings had been intensive and left only a few trees.

The density and origin of other stems in 1985 indicated that post-1914-20 regeneration had been abundant and come from a mixture of coppice and maidens. Coppice individuals were abundant and mainly of ash, field maple, hazel and common and midland hawthorn. The ash and field maple mainly had up to five large live stems present, whereas the hawthorn and hazel generally had more but smaller stems. Most oak individuals appeared to be derived from old stools, though overall it was scarce as coppice. Maidens (most of which were single-stemmed) were far less abundant than coppice individuals and included mainly ash with some birch and field maple.

Four larger snags of field maple (64-105cm gbh), an ash and oak (both 89cm gbh), and four hawthorn (42-48cm gbh) were present. In addition, many larger hazel stems were snags (including 23 of 44 sized 40-65cm gbh, 88 of 129 sized 30-<40cm gbh, and 181 of 306 sized 20-<30cm gbh), indicating that this species was in decline. Birch was also in decline: it was mainly grouped in section two on transect 9 and section nine on transect 18, and almost half of the 44 recorded trees were snags (including the five largest at 87-158cm gbh and five more sized 62-77cm gbh), leaving only two larger live birch (at 72-78cm gbh). Birch had many mature trees killed across the wood in the drought of 1976

Table 3.4.1: Basal area, density and size-class distribution for live individuals/stems recorded on the permanent transects in Monks Wood in 1985. Includes all individuals ≥1.3m height and all recorded stems

					Gbh size-class (cm) (n stems)										
		Basal area (m^2 ha^{-1})	Individuals (n ha^{-1})	Stems (n ha^{-1})	<10	10-<30	30-<50	50-<70	70-<90	90-<110	110-<130	130-<160	160-<190	190-<220	All sizes
Major trees	Ash	14.6	258	536	290	49	139	187	144	64	25	16	-	-	914
	Field maple	5.6	111	240	27	72	127	114	45	14	6	4	-	-	409
	Oak	2.9	22	25	1	-	3	1	3	14	8	7	4	2	43
Minor trees	Service	0.2	2	2	1	-	-	-	1	-	-	-	1	-	3
	Birch	0.1	11	12	2	9	7	-	2	-	-	-	-	-	20
	Aspen	<0.1	4	4	5	-	-	1	-	-	-	-	-	-	6
Major shrubs	Midland hawthorn	1.6	229	1137	882	1018	38	2	-	-	-	-	-	-	1940
	Hazel	1.3	193	1072	1204	562	57	6	-	-	-	-	-	-	1829
	Common hawthorn	1.2	94	418	306	334	58	11	3	1	-	-	-	-	713
Other species	Blackthorn	0.3	83	101	81	72	15	4	-	-	-	-	-	-	172
	Goat willow	0.2	8	12	1	3	13	4	-	-	-	-	-	-	21
	Crab apple	<0.1	2	4	-	2	2	2	1	-	-	-	-	-	7
	Dogwood	<0.1	79	96	128	35	1	-	-	-	-	-	-	-	164
	Privet	<0.1	128	140	236	2	-	-	-	-	-	-	-	-	238
	Elder	<0.1	4	9	5	11	-	-	-	-	-	-	-	-	16
	Spindle	<0.1	3	6	4	6	-	-	-	-	-	-	-	-	10
	Guelder rose	<0.1	1	4	7	-	-	-	-	-	-	-	-	-	7
	All species	28.0	1239	3817	3180	2175	460	332	199	93	39	27	5	2	6512

Several other minor trees and shrubs were also present: aspen was limited to just one live tree at 59cm gbh and a handful of small saplings from suckers; goat willow was prominent in two wetter areas close to rides along transect 18; only blackthorn, privet and dogwood were locally numerous amongst the shrubs; blackthorn at the start and end of transect 18 and in section 4 of transect 30; privet at the start of transect 18 and section 3 of transect 14; and dogwood at the end of transect 30 and section 5 of transect 30.

The basal area and density of stems in each section ranged from 18.2-32.3m^2 ha^{-1} and 1133-4817ha^{-1}. This reflected differences in the distribution of large trees, multi-stemmed understorey bushes, recent regeneration, large dead birch killed by the 1976 drought, and large collapsed stems. There was some variation in the species composition between transects and individual sections (see Figure 3.4.2). Ash was particularly frequent on transect 9 but many individuals here were small. It was scarce in several places on the other three transects. Ash basal area was higher on transects 9 and 14. Field maple was abundant only in places. Its basal area was highest on transect 18. Hawthorn was frequent in many but not all transect sections. The basal area of common hawthorn and midland hawthorn were highest on transects 14 and 18 respectively. Hazel was frequent and its basal area was highest on transect 9. It was frequent in many places on the other transects, but sometimes it was scarce. Variations within the transects were examined by comparing the basal area and density of live stems ≥5cm gbh in 26 available sections covering 592-600m^2 each (see Table 3.4.2). The basal area of ash was negatively correlated with oak, suggesting oak had tended to inhibit ash growth. The basal area of the main understorey shrubs (combined) and hazel (separately) were negatively correlated with the combined basal area of the main tree species, indicating that overstorey shading had restricted the understorey and particularly hazel (compare with Figure 3.4.2).

Figure 3.4.2: Distribution of ash, field maple, hawthorn and hazel individuals recorded on the four permanent transects in Monks Wood in 1986. Symbols show the location and species of each individual. Includes all individuals alive and ≥1.3m tall

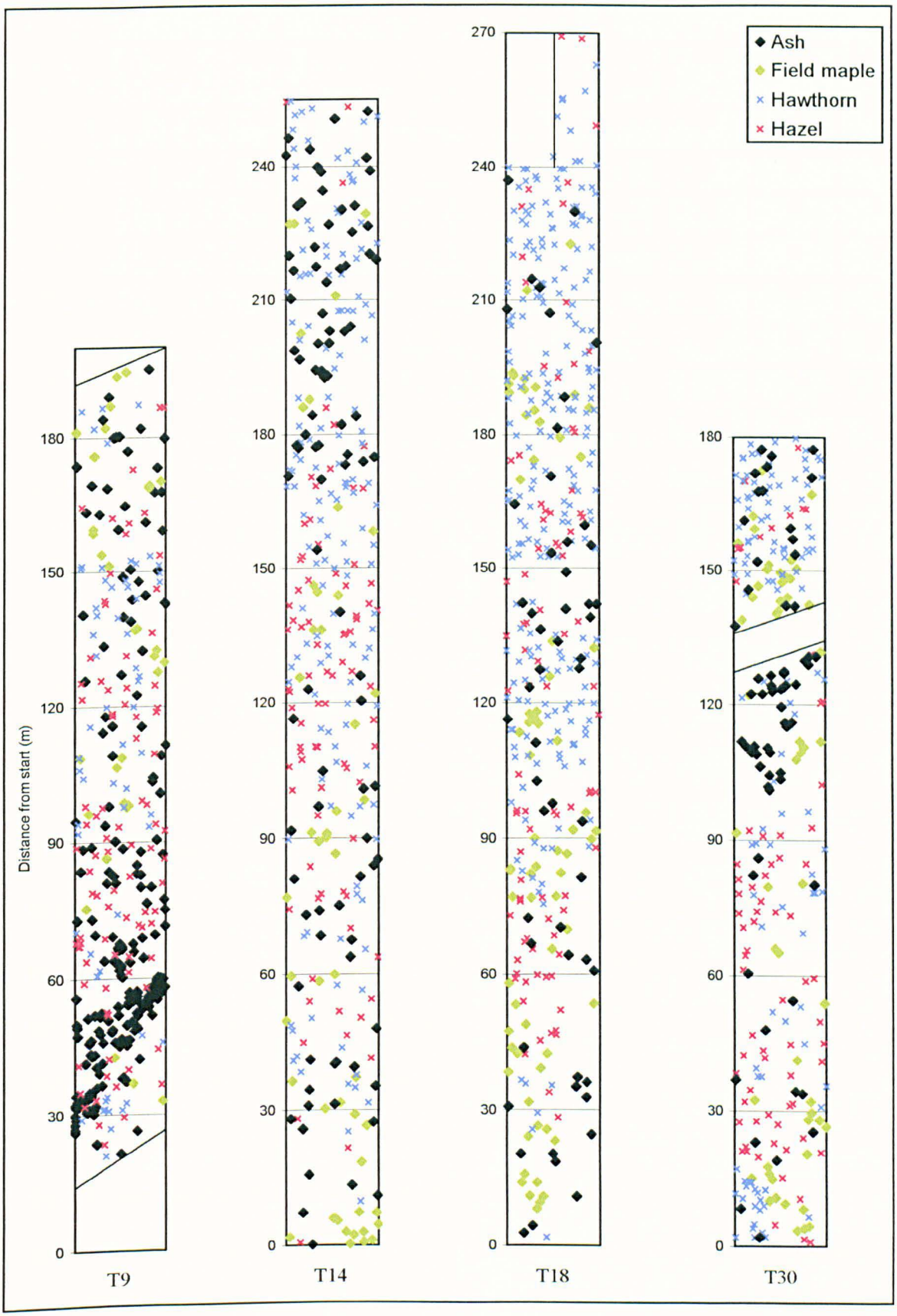


Table 3.4.2: Comparison of the stem basal area for the main tree and shrub species in 26 transect sections in Monks Wood in 1985 (includes all live stems ≥5cm gbh; all sections were 600m^2 except one of 592m^2). The table shows the Spearman rank correlation coefficients (r_s) (lower left half) and significance levels for these (upper right half) (*** = P<0.001, ** = P<0.01, * = P<0.05, ns = not significant)

	Field maple	Hazel	Common hawthorn	Midland hawthorn	Both hawthorns	Hazel & hawthorn	Ash	Oak	Ash, field maple & oak
Field maple	-	ns	ns	ns	*	ns	ns	ns	ns
Hazel	0.217	-	ns	ns	ns	**	ns	ns	*
Common hawthorn	-0.218	-0.326	-	ns	**	ns	ns	ns	ns
Midland hawthorn	-0.354	0.138	-0.031	-	***	***	ns	ns	ns
Both hawthorns	-0.405	-0.097	0.583	0.715	-	***	ns	ns	ns
Hazel & hawthorn	-0.353	0.531	0.267	0.654	0.733	-	ns	ns	*
Ash	-0.326	-0.360	0.155	-0.214	0.012	-0.164	-	*	**
Oak	-0.079	0.063	-0.032	0.262	0.079	0.033	-0.432	-	ns
Ash, field maple & oak	0.297	-0.391	-0.026	-0.322	-0.232	-0.475	0.602	0.063	-

The general scarcity gaps (as inferred by the lack of large snags) and size-distribution of live stems in 1985 indicated that competitive exclusion had been a major process beforehand. The size-distributions of the major tree and shrub species were mostly (but see discussion of ash and hazel below) normal with a strong right-skew (Table 3.4.1). These stems represented the remaining individuals from the cohort established soon after 1914-20, which had self-thinned over many decades to leave: (i) a few, dominant, fast-growing large-size stems; (ii) many suppressed, slow-growing, small-medium stems; and (iii) a paucity of very small stems which had declined most. Growth had been highest amongst the ash population, whose modal size-class in 1985 was 50-<70cm gbh, whereas this was only 30-<50cm gbh for field maple and 10-<30cm gbh for both hawthorn species.

Stem collapse appeared to have been a significant cause of demise, particularly for understorey stems that had grown outwards on a lean. This was evidenced by the presence of various stems in 1985 that remained alive but had fallen over. Most apparently to have snapped under their own weight (probably during windstorms) and had been leaning

already. Some represented entire stools or individuals, whereas others were secondary stems on coppice stools. They included a small number of ash, blackthorn, dogwood, elder, field maple, goat willow, hazel and privet, and a large number (129) of hawthorn stems. Nevertheless, only 19 were ≥30cm gbh, including six blackthorn, five hawthorn, five goat willow, and one each of ash, hazel and field maple. These combined with a number of recorded dead fallen stems that had suffered a similar fate.

Although the stands remained largely closed, there had been some recent regeneration, as revealed by the number of small stems/individuals recorded in 1985 (Table 3.4.1). These were principally of ash: seedlings of which were locally abundant in parts of transects 9 and 18, either where large birch snags/stumps stood (i.e. below gaps created by the 1976 drought), on the margins of rides, or where the understorey had part-collapsed; and saplings of which had grown to ≥1.3m height, including 80 in section 2 of transect 9 and about 40 others elsewhere. In addition, there appeared to have been a moderate amount of recent recruitment of small individuals of mainly dogwood and privet with a few aspen, blackthorn, field maple, hawthorn and hazel. On multi-stemmed stool it was possible that the smallest stems had recently established, and this was most obvious on hazel, which had a particularly high number of stems <10cm gbh on existing stools.

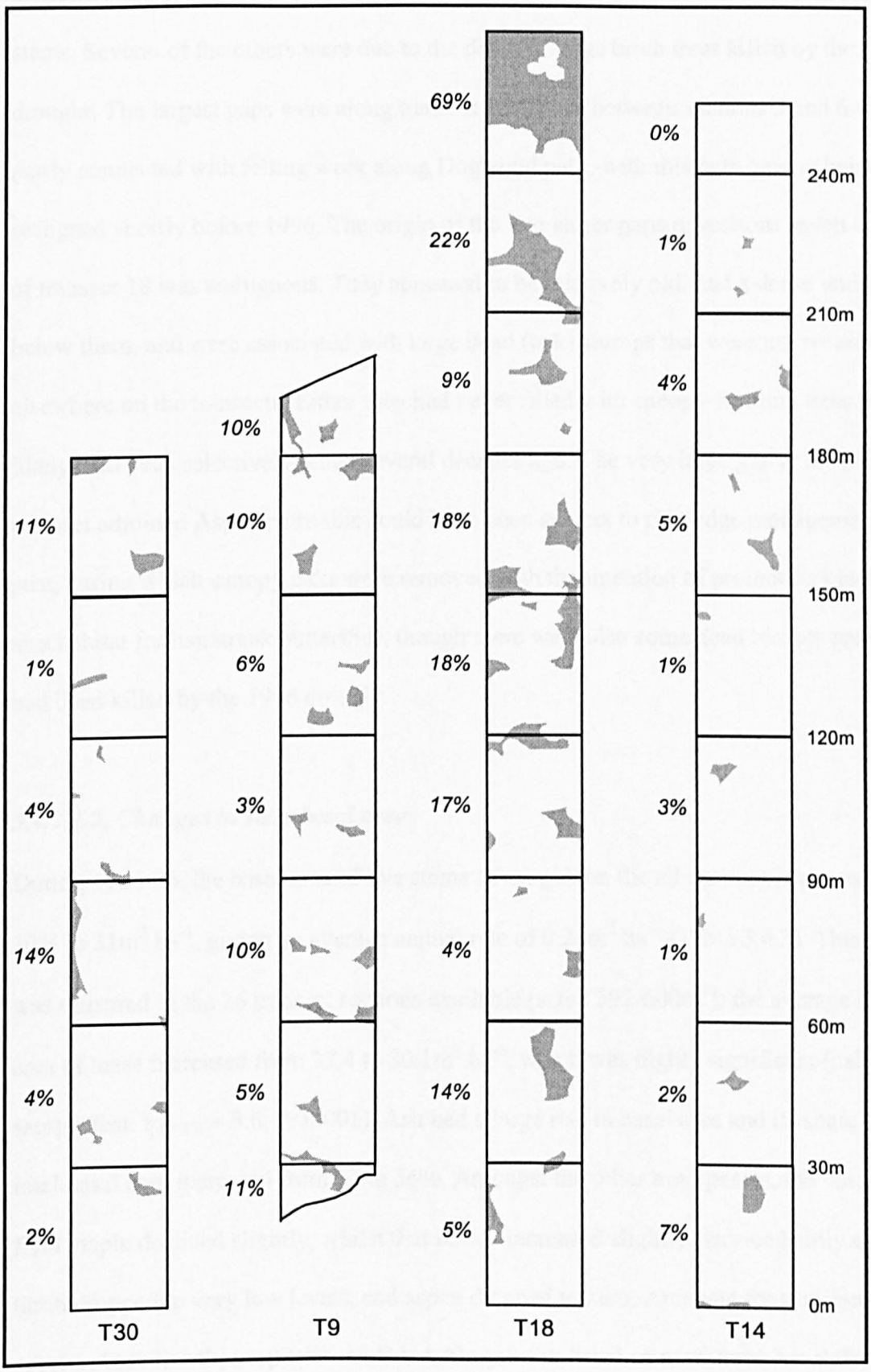
3.4.2.2. General aspects of stand change during 1985-96

3.4.2.2.1. Canopy gaps

Changes within the transects during 1985-96 were largely the result of natural processes within closed stands. Although ride management resulted in a small amount of disturbance, the affected mown strips and felled stems were largely excluded from the analysis.

Only a limited amount of canopy disturbance was evident prior to and during 1985-96. The fifty-five gaps recorded in 1996 covered only 9.5% of the total transect area (Figure 3.4.3).

Figure 3.4.3: Location of canopy gaps along the permanent transects in Monks Wood in 1996. The diagram is schematic but the transects and gaps are to scale. The transect number is shown at the bottom and the distance along to the right. The area occupied by gaps in each section is shown to the left as a percentage



Virtually all were filled below by understorey growth, which restricted the amount of light penetrating to the woodland floor. Many of the gaps were relatively small, scattered and caused by the death, die back, collapse or wind-snap of one or a few ash or field maple stems. Several of the others were due to the death of large birch trees killed by the 1976 drought. The largest gaps were along transect 18. Those between sections 5 and 6 were partly connected with felling work along Dogwood path, with this path having being partly realigned shortly before 1996. The origin of the two larger gaps in sections seven and eight of transect 18 was ambiguous. They appeared to be relatively old, had a dense understorey below them, and were associated with large dead (oak) stumps that were not recorded elsewhere on the transects. Either they had never filled with canopy-forming trees or, more likely, had been selectively felled several decades ago. The very large gap at the end of this transect adjoined Aspen path: this could have been subject to ride-edge management in the past, during which canopy oaks were removed with the intention of promoting blackthorn as a habitat for hairstreak butterflies, though there were also some dead birches present that had been killed by the 1976 drought.

3.4.2.2.2. Changes in stem basal area

During 1985-96, the basal area of live stems ≥5cm gbh on the all transect increased by 10% to 31m^2 ha^{-1}, giving an average annual rate of 0.26m^2 ha^{-1} (Table 3.4.3). This increase was mirrored in the 26 transect sections available (sized 592-600m^2): the average basal area of these increased from 27.4 to 30.1m^2 ha^{-1}, which was highly significant (paired-sample test: $t_{(df=25)} = 8.6$, $P<0.001$). Ash had a large rise in basal area and its share of the total basal area increased from 52 to 56%. Amongst the other tree species, the basal area of field maple declined slightly, whilst that of oak increased slightly, service hardly changed, birch dropped to very low levels, and aspen dropped to zero. Amongst the understorey species, both hawthorn species made notable gains in basal area, whereas hazel declined, as did blackthorn, crab apple, dogwood, guelder rose, spindle and goat willow.

Table 3.4.3: Change in the basal area, density and relative importance of live stems/ individuals recorded on the permanent transects in Monks Wood between 1985 and 1996. Includes all individuals ≥1.3m height, and all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

		Basal area (m^2 ha^{-1})		Individuals (n ha^{-1})		Stems (n ha^{-1})		Relative importance (%)	
		1985	1996	1985	1996	1985	1996	1985	1996
Major trees	Ash	14.6	17.2	258	200	391	382	32	35
	Field maple	5.6	5.4	118	106	233	199	14	12
	Oak	2.9	3.1	22	20	25	22	6	5
Minor Trees	Service	0.2	0.2	2	2	2	2	<1	<1
	Birch	0.1	<0.1	11	5	12	5	<1	<1
	Aspen	<0.1	-	4	-	1	-	<1	-
Major Shrubs	Midland hawthorn	1.6	1.9	229	207	1011	1042	19	21
	Hazel	1.3	1.2	193	143	838	700	16	14
	Common hawthorn	1.2	1.4	94	86	369	375	8	9
Minor species	Blackthorn	0.3	0.2	83	49	82	63	2	1
	Goat willow	0.2	0.1	8	6	12	10	<1	<1
	Privet	<0.1	<0.1	128	26	8	29	<1	<1
	Dogwood	<0.1	<0.1	79	21	47	30	<1	<1
	Elder	<0.1	<0.1	4	3	9	8	<1	<1
	Spindle	<0.1	<0.1	3	1	6	3	<1	<1
	Crab apple	<0.1	<0.1	2	2	4	4	<1	<1
	Guelder rose	<0.1	-	1	-	2	-	<1	-
	All species	28.0	30.9	1239	876	3051	2873	100	100

3.4.2.2.3. Changes in the density of stems/individuals

The density of live stems ≥5cm gbh decreased by 6% during 1985-96 (Table 3.4.3). This was mirrored in the 26 transect sections sized 592-600m^2, where the decrease in average stem density from 2998 to 2844ha^{-1} was significant (paired-sample test: $t_{(df=25)} = 2.0$, P = 0.03). Amongst the tree species, field maple and oak declined by 14-15%, whilst ash declined by only 2%. Birch density dropped by 60% and aspen completely died out, but service remained static. The two hawthorn species both increased in density, whilst hazel declined. Indeed, hazel had the greatest decline of all species in absolute terms, losing 138 stems ha^{-1} over 1985-96. Accordingly, both hawthorn species increased in relative importance, whereas hazel dropped. Amongst the minor understorey species, guelder rose died out, notable declines were recorded for blackthorn, dogwood and spindle (23-50%), crab apple, elder and goat willow declined slightly, but privet increased considerably as many stems grew over the 5cm gbh. The number of individuals ≥1.3m in height also

decreased during 1985-96 (Table 3.4.3). The greatest losses were for privet (101 ha^{-1}), followed by ash, dogwood and hazel (50-59 ha^{-1}), and then blackthorn (33 ha^{-1}). However, the 29% decline in individuals was far greater than the reduction in stems ≥5cm gbh. This was because many smaller individuals (with the main stem <5cm gbh) were lost.

3.4.2.2.4. Survival, mortality and recruitment patterns

The change in basal area and density of live individuals/stems was related to the survival, mortality and recruitment of stems. The fate and recruitment of live stems during 1985-96 is shown in Table 3.4.4. Of the 6512 live stems recorded in 1985, 67% remained alive in 1996. Survival was slightly higher for fallen than standing live stems (mortality rate, m = 2.36 v 3.55% a^{-1}). The overall mortality rate was 3.51% a^{-1}. Stems <5cm gbh in 1985 had by far the highest mortality rate, whilst stems ≥80cm gbh had the lowest rates (Table 3.4.5). A small number of losses, mostly privet, were reduced to low live growth <1.3m tall. Of those that died, 30% were still standing and formed snags in 1996. Stem loss was moderated because 702 stems recruited (i.e. grew to the ≥3cm gbh recording threshold). In some cases (mainly on hawthorn or hazel individuals) it was difficult to decide if these were actual recruits or had simply been omitted in 1985. Despite the presence of numerous small seedlings in 1985, only 20 new individuals managed to establish.

Survival, mortality and recruitment patterns differed among the species (Tables 3.4.4-5). Amongst the major tree species, mortality of ash was greater than oak and field maple. However, this was mainly due to the loss of numerous small-sized ash stems <5cm gbh: these accounted for 75% of ash losses. Excluding these, the mortality rate for ash was reduced to 0.99% a^{-1}: this compared to 1.36 and 1.72% a^{-1} for oak and field maple of the same size. The small ash losses included many of the recently established saplings recorded in 1985. Typically no trace could be found of these, indicating that muntjac deer had probably destroyed them. Mortality of ash decreased as the stem size increased and all

Table 3.4.4: Fate and recruitment of live stems/individuals on the permanent transects in Monks Wood between 1985 and 1996. The table shows the number of stems recorded in each category and the annual mortality rate (m). The number of fallen live stems in 1986 that survived is shown in superscript brackets in columns five and six. Includes all live stems in 1985

		1985		1985-96							
				Fate of 1985 stems by 1996					m rate	Recruits	
		Stems standing alive	Stems fallen alive	Standing alive	Fallen alive	Alive below 1.3m only	Died (snag)	Died (fallen)	% a^{-1}	New stems ≥3cm	New individuals
Major trees	Ash	912	2	640	$2^{(1)}$	2	37	233	3.1	19	5
	Oak	43	-	37	-	-	2	4	1.4	-	-
	Field maple	408	1	333	2	-	39	35	1.8	6	3
Minor trees	Service	3	-	3	-	-	-	-	zero	-	-
	Birch	20	-	8	-	-	5	7	8.0	-	-
	Aspen	6	-	-	-	-	-	6	all	-	-
Major shrubs	Midland hawthorn	1823	120	$1390^{(7)}$	$191^{(86)}$	1	124	237	1.9	266	1
	Common hawthorn	682	28	488	$86^{(26)}$	-	37	99	1.9	85	2
	Hazel	1823	6	960	$18^{(6)}$	-	345	506	5.5	291	1
Minor species	Crab apple	7	-	6	-	-	-	1	1.4	-	-
	Elder	7	9	3	$9^{(9)}$	-	2	2	2.6	2	-
	Goat willow	16	5	13	$2^{(1)}$	-	-	6	3.0	2	-
	Blackthorn	158	14	75	$23^{(11)}$	4	7	63	5.0	11	2
	Spindle	10	-	3	2	-	-	5	6.1	-	-
	Dogwood	155	9	37	$5^{(3)}$	-	7	115	11.7	11	1
	Privet	237	1	54	3	114	-	67	12.2	9	5
	Guelder rose	7	-	-	-	-	-	7	all	-	-
	All species	6317	195	$4050^{(7)}$	$343^{(143)}$	121	605	1393	3.51	702	20

Table 3.4.5: Mortality rate (m % a^{-1}) for stems of different sizes in the permanent transects in Monks Wood between 1985 and 1996. Includes all live stems recorded in 1985. Some size-classes were not represented (-) and in some classes all stems died

Gbh size-class (cm)	Ash	Field maple	Oak	Midland hawthorn	Common hawthorn	Hazel	All species
<5	14.52	4.78	-	1.93	1.84	8.34	8.15
5-<10	4.14	1.29	all died	1.79	1.78	5.02	3.41
10-<20	3.01	4.54	-	2.11	2.71	3.97	2.79
20-<40	2.14	2.29	6.11	1.00	1.10	6.53	2.66
40-<60	1.15	1.34	all died	0.00	0.52	7.80	1.57
60-<80	0.32	1.35	3.62	-	0.00	-	0.74
80-<100	0.11	0.00	1.07	-	0.00	-	0.14
100-<120	0.37	3.01	0.00	-	-	-	0.57
120-<140	0.00	0.00	1.07	-	-	-	0.34
140-<160	0.00	6.11	0.00	-	-	-	0.67
160-<220	-	-	0.00	-	-	-	0.00

ash over 120cm gbh in 1985 survived. Windblow accounted for most of the few large ash that died and exclusion for most of the small-medium stem losses. Many (64%) ash losses ≥10cm gbh remained as snags in 1996.

Most field maple losses were <80cm gbh and mortality rates tended to increase as stem size decreased. Exclusion appeared the main cause of death, but the largest field maple at 153cm gbh and another at 110cm gbh were windblown. About half of the field maple losses formed snags in 1996. Oak mortality was mainly of smaller sized stems that were excluded and formed snags in 1996. However, the largest tree lost was 128cm gbh and died standing but left a gap in the canopy, suggesting an additional cause of demise. A small number of ash and field maple stems and individuals managed to recruit. The new ash saplings were present as seedlings in 1985, as part of a group around two birch snags in section five of transect 9: these were the only ash seedlings of the many present that managed to grow up during 1985-96.

Amongst the major understorey species, hazel fared worst in terms of mortality (Tables 3.4.4-5). It had high mortality rates across all size-classes, though they were highest within

the very smallest and largest classes. Although 291 replacement stems recruited during 1985-96 and many stems increased in size, the number of stems sized 5-<10cm gbh fell from 805 to 482 and the number sized ≥30cm gbh fell from 63 to 45. The majority (60%) of stems that died had fallen by 1996. The two hawthorn species performed similarly: mortality rates were moderate and highest amongst the small and medium size-classes; numerous replacement stems recruited (mainly low trunk shoots and side-forks); many fallen stems persisted, including some that were on the ground in 1985; very few new individuals recruited; and around 70% of stems that died fell by 1996.

Many minor species had high mortality rates. All aspen and guelder rose stems died. Particularly high rates (m ≥10.0% a^{-1}) were found for blackthorn, dogwood and privet stems <5cm gbh and for blackthorn stems ≥40cm gbh. All birch <20cm gbh, 6 of 13 between 20-50cm gbh, and the two largest at 72-77cm gbh died. Although privet survival was poor, 114 of the 181 stems lost persisted as low-growing individuals in 1996, apparently having been eaten down by deer. In contrast, all service, most crab apple, and a moderate number of elder and goat willow stems survived.

3.4.2.2.5. Changes in established seedlings and other woody species

Approaching 600 established seedlings/bushes were recorded in the transects in 1985 (Table 3.4.6). These occurred mainly in localised groups scattered through the transects. They mainly represented advance regeneration seedling ash and suckers/seedlings of blackthorn, together with some low-growing dogwood and privet bushes. By 1996 virtually all of these individuals had died and many left no trace, suggesting deer had eaten them. Only a few ash seedlings had grown into saplings ≥1.3m tall, all of which were healthy but debarked by deer in 1996. Several privet survived and were joined by: (i) a large number of stems that had been reduced during 1985-96 by deer browsing, and (ii) a

few new bushes which could have been easily overlooked in 1985. Overall recruitment of new seedlings/bushes was minimal.

Table 3.4.6: Fate and recruitment of established seedlings/bushes (several years old and attaining 30cm height) and stems of other woody species in the permanent transects in Monks Wood between 1985 and 1996. Includes all live seedlings/bushes/stems recorded in 1985 and 1996. * = total estimated as some seedlings were simply recorded as part of a 'seedling group'

	1985		Fate 1985-96			Recruitment 1985-96	
	Bushes ≥1.3m tall	Established seedlings /bushes <1.3m tall	Sapling/ bush ≥1.3m tall	Seedling/ bush <1.3m tall	Dead	Not present in 1985	Alive ≥1.3m tall in 1985
Established seedlings							
Ash	-	369*	5	2	362	-	2
Blackthorn	-	131*	-	-	131	-	4
Privet	-	14*	-	5	9	6	109
Dogwood	-	10	-	-	10	-	-
Midland hawthorn	-	3	-	-	3	-	1
Oak	-	1	-	-	1	-	-
Total		574	5	7	562	6	116
Other woody species							
Bramble (short)		46*	-	-	46	2	2
Bramble (tall)	21			2	19	1	
Honeysuckle	2	-	-	-	2	-	
Rose	23	-	13	-	10	3	

Amongst the other woody species recorded in 1985, nearly all bramble were lost, apparently due to deer browsing. The only bramble attaining 1.3m in height in 1996 was growing over a collapsed hawthorn stool, where it was protected from deer browsing. Both honeysuckle and several roses were also lost, also possibly due to deer, with one of the surviving rose having been severely debarked by deer.

3.4.2.3. Stem growth during 1985-96

The analysis of stem gbh/basal area growth included only the main species. It combined stems from all transects. Two aspects were examined: (i) the relationship between the increment rate and initial size of stems; and (ii) the increment rate of stems in different crown position/size categories in 1996.

3.4.2.3.1. Main tree species

All the main tree species showed significant positive relationships between the gbh and basal area increment rates and the initial size of stems (i.e. larger stems generally increased more than smaller stems), albeit that some of the data was lognormal distributed (Figures 3.4.4-5, Table 3.4.7). For all species the regressions based on changes in basal area (rather than gbh) accounted for more of the variation, and in both cases ash had more variation included than oak or field maple. The relative position of the regression lines indicated that gbh and basal area increment rates overlapped considerably amongst the smaller size-classes for all species. However, as stem size increased, ash generally increased more than oak, and oak generally increased more than field maple.

Relationships between crown position/size and mean gbh/basal area increment were examined. It was expected that these would be positively related given that stem size generally increased as crown size got larger up through the canopy layers (Section 3.4.2). For ash there was a relatively clear progression, with larger crowned stems and those in the upper canopy layers having higher increment rates than smaller, overtopped stems (Table 3.4.8a). Oak showed a similar trend (Table 3.4.8b). The trend for field maple was less clear as most stems were overtopped, increments were low, and there was much variation within each category. For overtopped stems, crown size generally proved more important than position in determining the rank order of the increment rates (Table 3.4.8c).

3.4.2.3.2. Main shrub species

None of the main shrub species showed a significant relationship between the gbh increment rate and initial stem size. Although the basal area increment rates were significantly related to initial size, the regressions accounted for only 16-30% of the variation (Table 3.4.9). The best fitting regression for midland hawthorn took a linear form, whereas for common hawthorn and hazel an additional quadratic term proved

Figure 3.4.4: Relationship between the gbh increment and initial gbh of stems for the main tree species in the permanent transects in Monks Wood over 1985-96. Symbols/lines in blue = ash, red = oak, black = field maple. Parameters for the regression lines shown are given in Table 3.4.7. Some symbols represent more than one stem

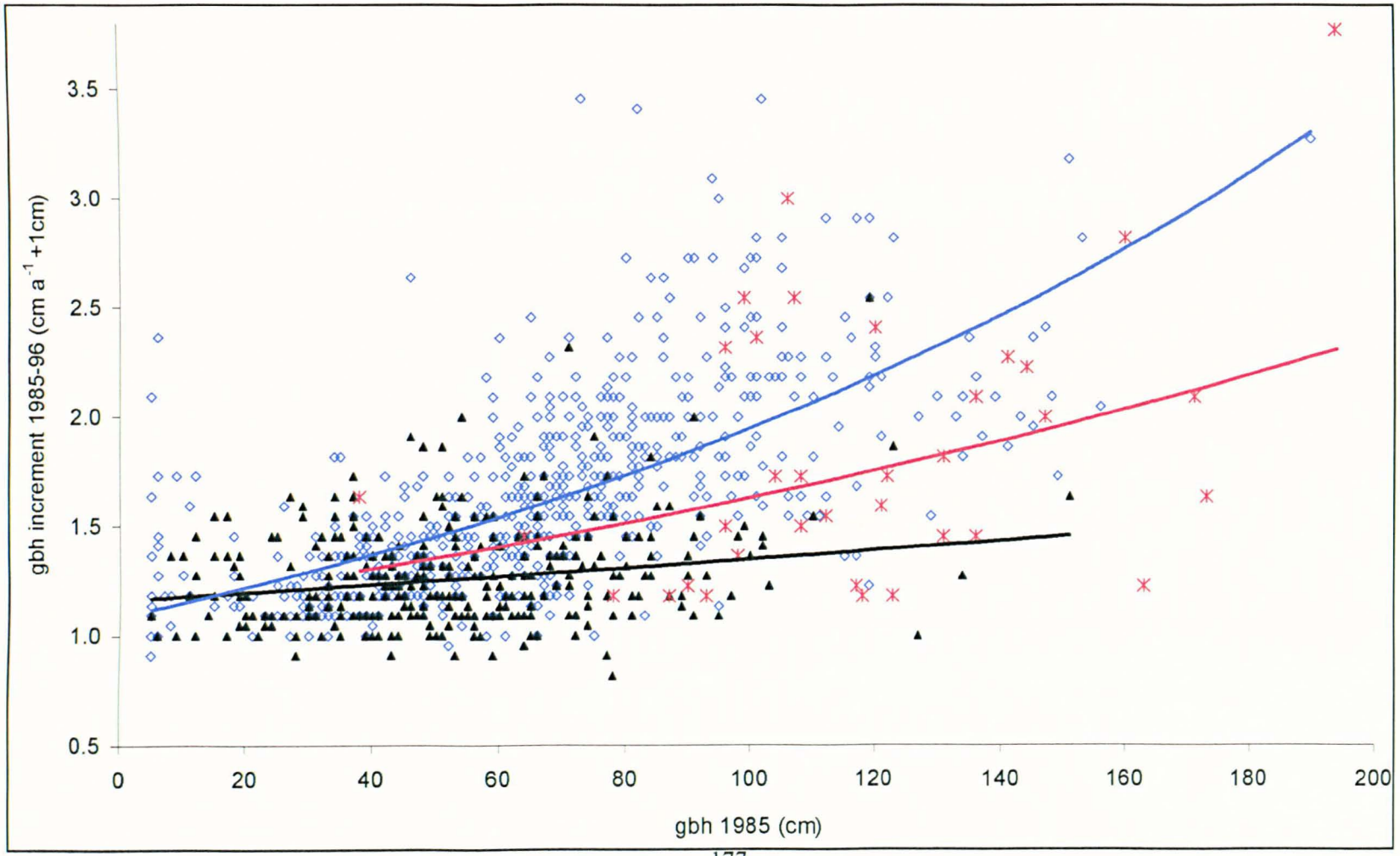


Figure 3.4.5: Relationship between the basal area increment and initial basal area of stems for the main tree species in the permanent transects in Monks Wood over 1985-96. Symbols/lines in blue = ash, red = oak, black = field maple. Parameters for the regression lines shown are given in Table 3.4.7. Some symbols represent more than one stem

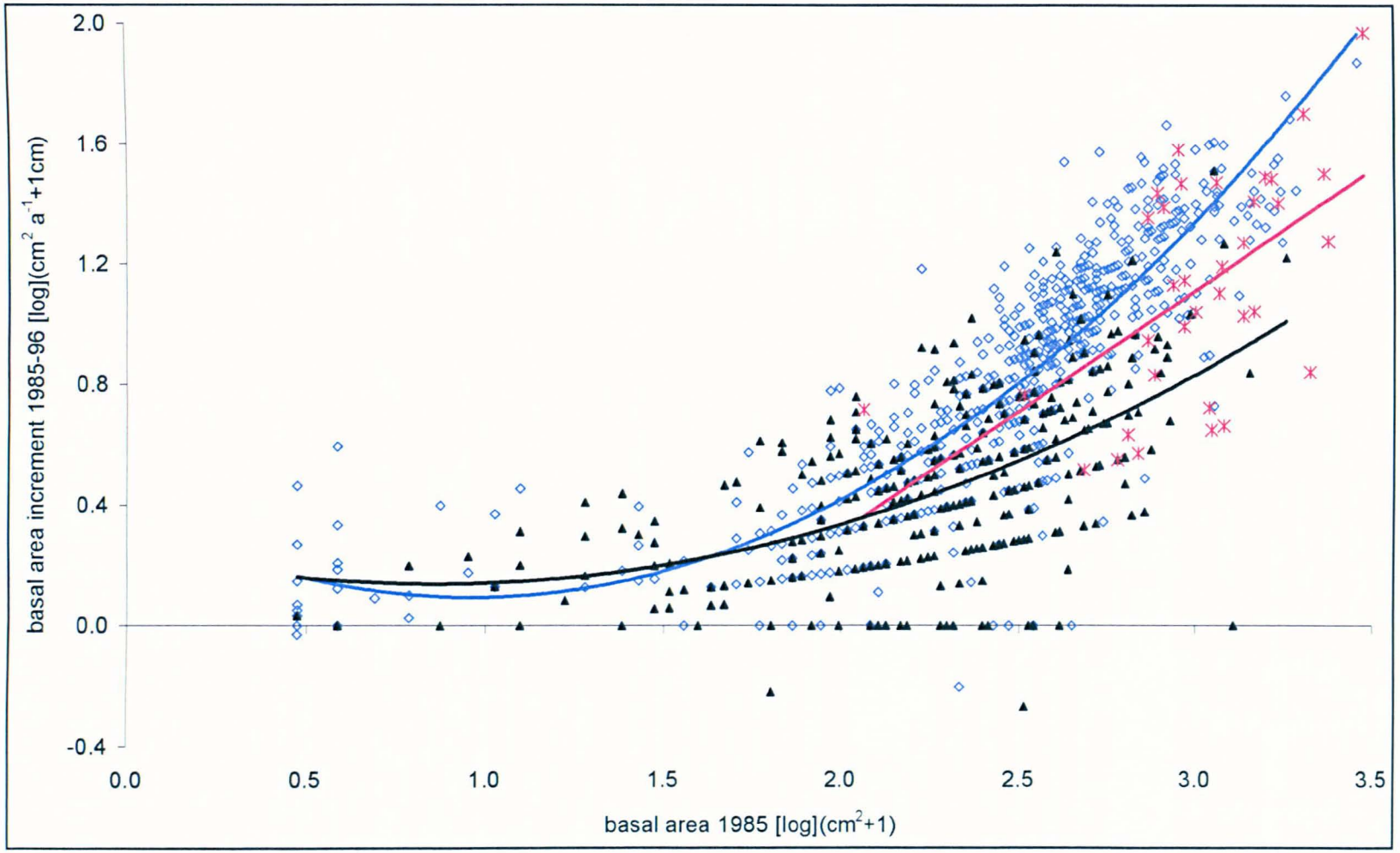


Table 3.4.7: Results of the stem increment analysis for the main canopy/sub-canopy tree species in the permanent transects in Monks Wood over 1985-96. The table shows the regressions comparing gbh increment (inc_{gbh}, cm a^{-1}) against initial gbh (ini_{gbh}, cm), and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2). Lognormal data were transformed before analysis. Figures 3.4.4-5 show the relationships as scatter plots

1. Gbh increment		**n**	**F**	**P**	**r^2%**
Ash	$\log(inc_{gbh+1}) = 0.00255.ini_{gbh} + 0.0350$	624	525.2	<0.001	45.8
Oak	$\log(inc_{gbh+1}) = 0.00161.ini_{gbh} + 0.0518$	36	5.8	=0.022	14.5
Field maple	$\log(inc_{gbh+1}) = 0.00066.ini_{gbh} + 0.0641$	317	14.9	<0.001	4.5
2. Basal area increment					
Ash	$\log(inc_{ba+1}) = 0.2999.\log(ini_{ba+1})^2 - 0.5753.\log(ini_{ba+1}) + 0.3696$	624	912.0	<0.001	74.6
Oak	$\log(inc_{ba+1}) = 0.8026.\log(ini_{ba+1}) - 1.2955$	36	16.2	<0.001	32.3
Field maple	$\log(inc_{ba+1}) = 0.2585.\log(ini_{ba+1})^2 - 0.1509.\log(ini_{ba+1}) + 0.2491$	312	74.4	<0.001	32.5

Table 3.4.8: Comparison of the increment rates over 1985-96 for stems in various crown position/size categories in 1996 for the three main tree species in the permanent transects in Monks Wood. The table shows: (i) the median rate and mean rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the mean ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Ash ($H_{gbh(df=5)}$ = 419.1, $H_{basal\ area(df=5)}$ = 499.0, both P<0.001)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Canopy with large crown	11	1.18	543.4	=bc; >def (Q≥5.43)***
(b) Canopy with medium crown	83	1.18	534.6	=a; >cdef (Q≥4.71)***
(c) Canopy with small crown	198	0.82	423.8	=a; <b; >def (Q≥8.60)***
(d) Canopy with very small crown	149	0.46	238.2	<abc; =e; d>f (Q=5.21)***
(e) Sub-canopy all crown sizes	46	0.36	170.4	<abc; =df
(f) Understorey & ground all crown sizes	137	0.18	127.2	<abcd; =e
2. Basal area increment rates				
(a) Canopy with large crown	11	26.80	594.3	=b; >c (Q=3.03)*; >def (Q≥6.16)***
(b) Canopy with medium crown	83	21.54	556.1	=a; >cdef (Q≥5.55)***
(c) Canopy with small crown	198	10.36	425.3	=a; <b; >def (Q≥8.44)***
(d) Canopy with very small crown	149	4.12	247.1	<abc; =e; >f (Q=7.07)***
(e) Sub-canopy all crown sizes	46	2.64	176.3	<abc; =df
(f) Understorey & ground all crown sizes	137	1.07	96.2	<abcd; =e

(b) Oak ($H_{gbh(df=3)}$ = 21.3, $H_{basal\ area(df=3)}$ = 27.6, both P<0.001)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Canopy with large crown	4	1.52	34.5	=b; >c (Q=2.98)*; >d (Q=3.54)**
(b) Canopy with medium crown	16	1.07	27.0	=a; >c (Q=2.85)*; >d (Q=3.48)**
(c) Canopy with small/very small crown	13	0.50	14.6	<ab; =d
(d) Sub-canopy & understorey all crown sizes	7	0.23	8.6	<ab; =c
2. Basal area increment rates				
(a) Canopy with large crown	4	39.96	37.7	=b; >c (Q=3.52)**; >d (Q=4.23)***
(b) Canopy with medium crown	16	23.06	27.3	=a; >c (Q=3.00)*; >d (Q=3.89)***
(c) Canopy with small/very small crown	13	7.86	14.2	<ab; =d
(d) Sub-canopy & understorey all crown sizes	7	3.30	6.7	<ab; =c

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Table 3.4.8: continued

(c) Field maple ($H_{gbh\ (df=9,306)} = 60.4$, $H_{basal\ area\ (df=9,306)} = 129.7$, both $P<0.001$)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Canopy with medium crown	4	0.75	275.1	=bcdefghi; >j (Q=3.49)*
(b) Understorey with large crown	10	0.46	253.7	=acdefg; >hj (Q≥3.48)*; >i (Q=4.62)***
(c) Canopy with small crown	27	0.41	222.8	=abdefg; >hj (Q≥3.27)*; >i (Q=5.44)***
(d) Sub-canopy with medium crown	6	0.34	212.1	=abcefghij
(e) Understorey with medium crown	96	0.27	170.7	=abcefghj; >i (Q=4.21)**
(f) Canopy with very small crown	29	0.23	159.4	=abcefghij
(g) Sub-canopy with small crown	36	0.23	160.2	=abcefghij
(h) Sub-canopy with very small crown	20	0.18	125.6	<abc; =efghij
(i) Understorey with small/very small crown	79	0.09	112.6	<abc; =efghij
(j) Ground all crown sizes	9	0.09	108.4	<abc; =efghij
2. Basal area increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Canopy with medium crown	4	16.60	306.7	=bcdefg; >h (Q=3.27)*; >ij (Q=4.65)***
(b) Understorey with large crown	10	5.87	273.6	=acdef; >gh (Q≥3.61)*; >ij (Q=5.51)***
(c) Canopy with small crown	27	5.32	259.4	=abde; >f (Q=3.73)*; >ghij (Q≥4.31)***
(d) Sub-canopy with medium crown	6	3.91	249.8	=abcefgh; >i (Q=4.16)**; >j (Q=4.31)***
(e) Canopy with very small crown	29	2.37	185.8	=abcdfgh; >i (Q=4.88)**; >j (Q=4.11)*
(f) Sub-canopy with small crown	36	1.97	172.6	<c; =abcdeghij
(g) Understorey with medium crown	96	1.95	163.9	<c; =abdefhj; >i (Q=3.90)**
(h) Sub-canopy with very small crown	20	1.77	143.2	<abc; =defghij
(i) Understorey with small/very small crown	79	0.60	89.1	<abcdeg; =fhj
(j) Ground all crown sizes	9	0.21	42.5	<abcde; =fghi

Table 3.4.9: Results of the stem increment analysis for the main shrub species in the permanent transects in Monks Wood over 1985-96. The table shows the regressions comparing basal increment (inc_{ba}, $cm^2\ a^{-1}$) against initial basal area (ini_{ba}, cm^2). The regressions of gbh increment (inc_{gbh}, $cm\ a^{-1}$) on initial gbh (ini_{gbh}, cm) were not significant. Lognormal data were transformed before analysis. Figure 3.4.6 shows the basal area relationships as a scatter plot

Basal area increment		n	F	P	r^2 %
Common hawthorn	$\log(inc_{ba+1}) = 0.1607.\log(ini_{ba+1})^2 - 0.2658.\log(ini_{ba+1}) + 0.2454$	316	57.6	<0.001	26.9
Midland hawthorn	$\log(inc_{ba+1}) = 0.1126.\log(ini_{ba+1})^2 - 0.1311.\log(ini_{ba+1}) + 0.1413$	912	63.6	<0.001	12.3
Hazel	$\log.(inc_{ba+1}) = 0.1515.\log(ini_{ba+1}) + 0.0738$	750	109.4	<0.001	12.8

significant. A visual comparison of the position of the basal area regression lines (see Figure 3.4.6) revealed that they were at similar positions.

The increment rates of the main shrub species in the various crown position/size categories showed the same general trend (Table 3.4.10). Although there was considerable variation in the rates within each group and some of the group means did not differ significantly, stems with large or medium crowns generally increased more than those with small or very small crowns, and stems with comparable sized crowns in the understorey generally increased more than those in the ground layer.

Figure 3.4.6: Relationship between the basal area increment and initial basal area of stems for the main shrub species in the permanent transects in Monks Wood over 1985-96. Symbols/lines in blue = hazel, red = common hawthorn, black = midland hawthorn. Parameters for the regression lines shown are given in Table 3.4.10. Some symbols represent more than one stem

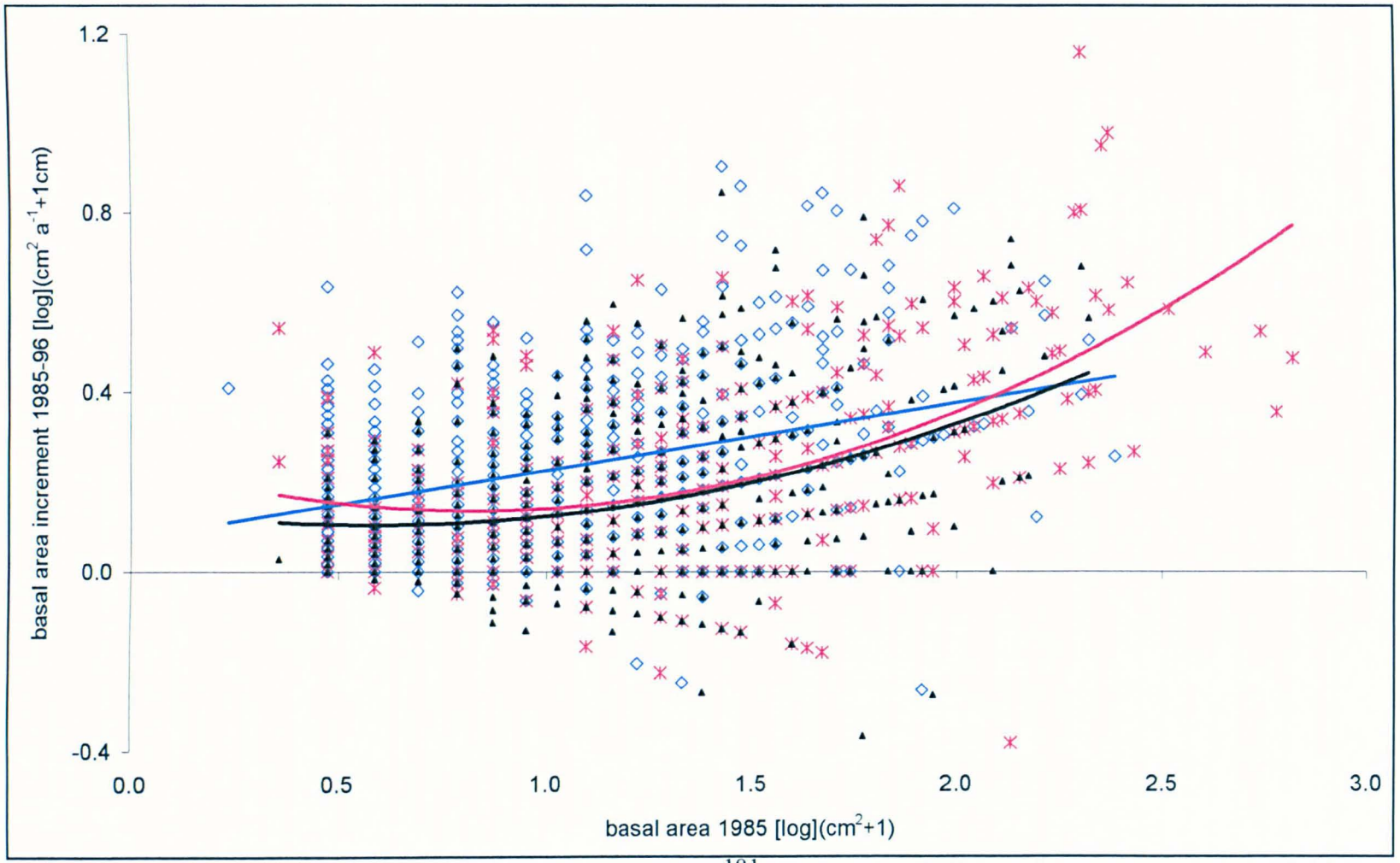

Table 3.4.10: Comparison of the increment rates over 1985-96 for stems in various crown position/size categories in 1996 for the three main shrub species in the permanent transects in Monks Wood. The table shows: (i) the median rate and mean rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the mean ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Common hawthorn ($H_{gbh(df=6)}$ = 63.0, $H_{basal\ area\ (df=6)}$ = 140.6, both P<0.001)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	50	0.36	215.4	=bcd; >efg (Q≥4.82)***
(b) Understorey with small crown	114	0.23	179.6	=acd; >ef (Q≥3.36)**; >g (Q=5.39)***
(c) Understorey with large crown	4	0.21	181.1	=abdefg
(d) Ground with large/medium crown	15	0.18	170.3	=abcef; >g(Q=3.12)*
(e) Understorey with very small crown	82	0.16	135.4	<ab; =cdfg
(f) Ground with very small crown	19	0.09	97.2	<ab; =cdeg
(g) Ground with small crown	32	0.05	81.6	<abd; =cef
2. Basal area increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	50	2.29	258.7	=bc; >d (Q=3.45)*; >efg (Q=7.29)***
(b) Understorey with small crown	114	2.03	272.0	=ac; >defg (Q≥4.22)***
(c) Understorey with large crown	4	0.80	181.4	=abdefg
(d) Ground with large/medium crown	15	0.52	166.1	<ab; =cef; >g(Q=3.45)*
(e) Understorey with very small crown	82	0.29	112.5	<ab; =cdfg
(f) Ground with very small crown	19	0.09	79.4	<ab; =cdeg
(g) Ground with small crown	32	0.08	67.4	<abd; =cef

(b) Midland hawthorn ($H_{gbh(df=6)}$ = 103.5, $H_{basalarea\ (df=6)}$ = 208.9, both P<0.001)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	32	0.46	679.4	=bce; >dfg (Q≥4.95)***
(b) Ground with medium crown	43	0.27	579.2	=ace; >d (Q=3.30)*; >fg (Q≥4.27)***
(c) Understorey with small crown	222	0.23	547.0	=abe; >dfg (Q≥4.78)***
(d) Understorey with very small crown	338	0.18	438.3	<abc; =ef; >g(Q=4.26)***
(e) Ground with large crown	4	0.09	438.4	=abcdfg
(f) Ground with small crown	179	0.09	388.1	<abc; =deg
(g) Ground with very small crown	94	0.05	307.4	<abcd; =ef
2. Basal area increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	32	1.76	795.0	=d; >cb (Q≥3.26)*; >efg (Q≥=7.74)***
(b) Ground with medium crown	43	0.76	594.5	<a; =dc; >efg (Q≥4.14)***
(c) Understorey with small crown	222	0.61	596.5	<a; =bd; >efg (Q≥7.84)***
(d) Ground with large crown	4	0.42	612.6	=acdefg
(e) Understorey with very small crown	338	0.27	418.3	<abc; =df; >g (Q=4.70)***
(f) Ground with small crown	179	0.15	353.7	<abc; =deg
(g) Ground with very small crown	94	0.09	274.2	<abce; =df

(c) Hazel ($H_{gbh\ (df=5)}$ = 164.8, $H_{basal\ area\ (df=5)}$ = 280.9, both P<0.001)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	37	0.68	576.0	=c; >b (Q=2.97)*; >def (Q≥7.14)***
(b) Understorey with small crown	310	0.46	464.3	<a; =c; >def (Q≥6.51)***
(c) Ground with medium crown	7	0.32	379.4	=abdef
(d) Understorey with very small crown	314	0.23	308.0	<ab; =cf; >e (Q=2.99)*
(e) Ground with small crown	50	0.13	209.7	<abd; =cf
(f) Ground with very small crown	32	0.09	203.5	<ab; =cde
2. Basal area increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Understorey with medium crown	37	2.43	657.5	>c (Q=3.61)**; >bdef (Q≥4.44)***
(b) Understorey with small crown	310	0.90	490.3	<a; =c; >def (Q≥7.94)***
(c) Ground with medium crown	7	0.54	334.9	<a; =bdef
(d) Understorey with very small crown	314	0.33	283.6	<ab; =cdf; >e (Q=3.50)**
(e) Ground with small crown	50	0.17	168.3	<abd; =cf
(f) Ground with very small crown	32	0.13	170.9	<ab; =cde

3.4.2.4. Condition of stems in 1996

3.4.2.4.1. Stratification, crown size and crown die back

All live stems were given a crown position, crown size and die back category in 1996 (Table 3.4.11). The canopy layer accounted for only 10% of stems, but 21% of these had medium or large crowns. In the lower three layers, the sub-canopy contained the least number of stems, but the understorey and ground layers accounted for many stems. In the lower layers most stems had small or very small crowns.

Table 3.4.11: Crown position and crown size for all live stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows the number of stems in a particular crown position and the percentage of stems in each column with different crown sizes

	Canopy	Sub-canopy	Understorey	Ground
Ash	412	44	163	42
Field maple	60	59	191	31
Oak	31	4	2	-
Midland hawthorn	-	-	968	878
Hazel	-	-	962	307
Common hawthorn	-	-	397	262
Other species	7	4	121	147
All species	510	111	2804	1667
Crown size				
% large	3	-	1	1
% medium	18	8	9	9
% small	44	44	34	49
% very small	35	48	57	41

Ash dominated the canopy layer and accounted for 40% of stems were in the sub-canopy. It was, however, relatively scarce in the lowest two layers. Stratification and die back of ash are detailed in Table 3.4.12. The larger crowned trees in the canopy accounted for most of the largest gbh trees and nearly all of these had no major die back. Progressively downwards through the canopy layers and as crown size was reduced within each layer, the gbh size-range/mode decreased whilst the degree of die back generally increased. Thus, the smallest gbh stems within each layer tended to have the smallest crowns and most die back. The (limited number of) surviving ash saplings/seedlings from the cohort that had developed in abundance in 1985, included many of the smaller crowned ash <10-(20)cm

Table 3.4.12: Relationship between stem size, crown position and die back for all live ash stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate [(m)] or severe/very severe die back [(s)]; (iii) the number of larger stems that were fallen alive on ground [(F)] or were snapped/tipped and hung-up [(S)]. The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Canopy				Sub-canopy			Understorey				Ground		
Crown size: Gbh size-class (cm)	Large	Medium	Small	Very small	Medium	Small	Very small	Large	Medium	Small	Very small	Medium	Small	Very small
3-9.9	-	-	-	-	-	-	-	-	-	-	42 (4m)	-	15 (1m)	18 (9m,1s)
10-19.9	-	-	-	-	-	-	-	-	-	3 (2m)	11 (3m,2s)	-	4 (4m)	1 (1s)
20-29.9	-	-	-	-	-	-	1	-	2 (2m)	9 (3m,3s)	5 (1m,4s)	-	-	1 (1s)
30-39.9	-	-	-	2	-	-	2 (1m)	-	5 (1m,2s)	36 (14m,19s)	7 (7s)	-	-	-
40-49.9	-	-	-	14 (7m)	-	5	11 (6m,4s)	-	9 (3m,2s)	12 (2m,10s)	2 (2s)	-	1 (1sF)	1 (1s)
50-59.9	-	-	3 (1m)	35 (21m)	-	3 (2m)	9 (8m,1s)	-	5 (3m)	4 (4s)	1 (1s)	-	-	-
60-69.9	-	-	14 (2m)	40 (22m)	1	4 (2m,1s)	4 (3m)	-	1 (1s)	3 (3s)	2 (2s)	-	-	-
70-79.9	-	-	44 (5m)	34 (17m,2s)	-	1	1 (1m)	1 (1m)	1 (1m)	1	1 (1sS)	1 (1sF)	-	-
80-89.9	-	1	62 (6m)	15 (10m)	-	-	1 (1m)	-	-	-	-	-	-	-
90-99.9	-	7	30 (4m)	3 (1m)	-	-	-	-	-	-	-	-	-	-
100-109.9	-	15	18 (6m)	-	-	-	-	-	-	-	-	-	-	-
110-119.9	-	18	14 (4m)	-	-	-	1 (1sS)	-	-	-	-	-	-	-
120-129.9	-	13	-	-	-	-	-	-	-	-	-	-	-	-
130-139.9	1	12	1 (1m)	-	-	-	-	-	-	-	-	-	-	-
140-149.9	1	4	-	-	-	-	-	-	-	-	-	-	-	-
150-159.9	3 (1m)	2	-	-	-	-	-	-	-	-	-	-	-	-
160-169.9	4	-	-	-	-	-	-	-	-	-	-	-	-	-
170-179.9	1	1	-	-	-	-	-	-	-	-	-	-	-	-
All sizes	10	73	186	142	1	13	30	1	23	68	71	1	20	21
Die back														
% healthy/part	90	100	87	44	100	62	13	-	35	12	62	-	70	38
% moderate	10	-	13	55	-	31	67	100	43	31	11	-	25	43
% severe/very severe	-	-	-	1	-	8	20	-	22	57	27	100	5	19

gbh, some of which had grown into the understorey and remained healthy. Most die back appeared to be due to competition for growing space in the overstorey and shading in the lower stratum. A few wind-damaged trees, however, had suffered substantial crown loss a few were tipped over and recorded in the understorey or ground layers.

Field maple was mainly recorded in the understorey. However, it accounted for slightly over half the stems in the sub-canopy and 12% of canopy stems. Although many of its stems had small or very small crowns and crown die back was widespread (Table 3.4.13), a high proportion retained medium-sized crowns in the understorey. Again, the smallest gbh stems within each layer tended to have the smallest crowns and more die back, and the very smallest were in the lowest layers.

Comparing the relative frequency of ash versus field maple stems: ash was more frequent in the canopy and field maple in the other layers (412 of 661 ash v 60 of 341 field maple stems in canopy; $\chi^2_{(df=1)} = 180.7$, $P<0.001$); and ash was more frequent with moderate or worse die back both for small/very small crowned stems in the canopy (109 of 328 ash v 18 of 136 field maple stems; $\chi^2_{(df=1)} = 19.3$, $P<0.001$) and for all stems in the other layers (152 of 249 ash v 134 of 281 field maple stems; $\chi^2_{(df=1)} = 9.5$, $P<0.01$). Die back was mainly due to exclusion, but a few stems in the lower layers and had much die back because they had been wind-damaged, including a few larger gbh stems mainly of ash.

Oak was mainly recorded in the canopy. Although it accounted for only 6% of trees in this layer, 19 had medium or large crowns (Table 3.4.14). Surprisingly few oak showed signs of die back, save for one larger tree that had been relegated to the sub-canopy after much die back due to an unknown cause. Again, the smallest gbh stems within each layer tended to have the smallest crowns and the very smallest were in the sub-canopy or understorey.

Table 3.4.13: Relationship between stem size, crown position and die back for all live field maple stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate [(m)] or severe/very severe die back [(s)]; (iii) the number of larger stems that were fallen alive on ground [(F)] or were snapped/tipped and hung-up [(S)]. The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Canopy			Sub-canopy			Understorey				Ground		
Crown size: Gbh size-class (cm)	Medium	Small	Very small	Medium	Small	Very small	Large	Medium	Small	Very small	Medium	Small	Very small
3-9.9	-	-	-	-	-	-	-	-	-	-	1	12 (2m)	7 (2m)
10-19.9	-	-	-	-	-	-	-	1	8 (1m,2s)	1 (1s)	3	7 (1m)	-
20-29.9	-	-	-	-	-	-	-	3	21 (4m,8s)	2 (2s)	-	-	1 (1s)
30-39.9	-	-	-	-	-	-	-	13 (1m)	19 (9m,5s)	1 (1sS)	-	-	-
40-49.9	-		1 (1m)	-	4 (1m)	5 (4m,1s)	-	33 (5m,4s)	18 (3m,12s,1sS)	3 (1m,2s)	-	-	-
50-59.9	-	1	7 (1m)	-	7 (1m)	6 (2m,1s)	2 (1m)	22 (4m,3s)	9 (3m,6s)	2 (1s,1sS)	-	1 (1sF)	-
60-69.9	-	2 (1m)	8 (4m)	1	13 (5m)	5 (3m,2s)	1	16 (5m,5s)	1 (1m)	-	-	-	-
70-79.9	-	3 (1m)	4 (1m)	3	9 (4m,1s)	2 (1s)	1	5 (2m,1s)	1 (1m)	-	-	-	-
80-89.9	-	8 (1m)	5 (2m)	1 (1m)	1	1 (1m,1s)	3 (1m)	1 (1s)	-	-	-	-	-
90-99.9	-	6	2 (2m)	-	-	1	2	1	-	-	-	-	-
100-109.9	-	5	1 (1m)	-	-	-	1	-	-	-	-	-	-
110-119.9	-	1 (1m)	-	-	-	-	-	-	-	-	-	-	-
120-129.9	-	-	1 (1m)	-	-	-	-	-	-	-	-	-	-
130-139.9	3	1 (1m)	-	-	-	-	-	-	-	-	-	-	-
140-149.9	-	-	-	-	-	-	-	-	-	-	-	-	-
150-159.9	1	-	-	-	-	-	-	-	-	-	-	-	-
All sizes	4	27	29	5	34	20	10	95	77	9	4	20	8
Die back													
% healthy/part	100	81	55	80	65	20	80	67	27	-	100	80	63
% moderate	-	19	45	20	32	30	20	18	29	11	-	15	25
% severe/very severe	-	-	-	-	3	50	-	15	44	89	-	5	12

Table 3.4.14: Relationship between stem size, crown position and die back for all live oak stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate [(m)] or severe/very severe die back [(s)]. The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Canopy				Sub-canopy			Understorey	
Crown size: Gbh size-class (cm)	Large	Medium	Small	Very small	Medium	Small	Very small	Large	Small
40-59.9	-	-	-	-	-	-	-	-	1
60-79.9	-	-	-	-	1	-	-	-	-
80-99.9	-	-	1	-	1	1	-	1	-
100-119.9	-	3	7	1	-	-	-	-	-
120-139.9	-	5	1 (1m)	2 (2m)	-	-	-	-	-
140-159.9	1	4	-	-	-	-	1 (1s)	-	-
160-179.9	-	1	-	-	-	-	-	-	-
180-199.9	2	1	-	-	-	-	-	-	-
200-239.9	2	-	-	-	-	-	-	-	-
All sizes	5	14	9	3	2	1	1	1	1
Die back									
% healthy/part	100	100	89	33	100	100	-	100	100
% moderate	-	-	11	67	-	-	-	-	-
% severe/very severe	-	-	-	-	-	-	100	-	-

The two hawthorn species accounted for 49% of stems in the understorey (35% midland, 14% common) and 69% of stems in the ground layer (53% midland, 16% common). None were tall enough to classify in the upper two layers. They showed similar patterns of stratification and die back (Table 3.4.15), in that smaller gbh stems tended to have smaller crowns, more die back and be in the ground layer, and that the ground layer included a few larger stems that had collapsed or been broken by falling canopy ash, which combined with numerous smaller stems of both species that were growing along the ground, laterally or with a distinct lean but remained alive (typically these were splayed stems on complex multi-stemmed stools). Although there was no major differences between the two species in terms of die back, common hawthorn was relatively more frequent than midland hawthorn in the understorey (397 of 659 stems v 968 of 1846 stems; $\chi^2_{(df=1)} = 11.9$, $P<0.001$), and in this layer accounted for most of the large or medium crowned stems (56 of 88 stems) and relatively few of the very small crowned stems (195 of 766 stems).

Hazel accounted for just over a third of the understorey stems, but only 18% of stems in the ground layer. Stem die back tended to be more prevalent amongst smaller crowned stems and the smallest stems were moreover in the ground layer (Table 3.4.16). Few stems had particularly large crowns or were fallen alive. Some, particularly the larger stems, were growing with a distinct lean and a lateral crown, whereas most small stems, including low trunk shoots, were generally growing more-or-less vertically. Comparing the relative frequency of hawthorn and hazel stems: hazel was much less frequent in the ground layer (307 of 1269 stems v 1140 of 2505 stems; $\chi^2_{(df=1)} = 161.9$, $P<0.001$), had slightly less stems with large or medium crowns (51 of 1269 stems v 215 of 2505 stems; $\chi^2_{(df=1)} = 26.8$, $P<0.001$), and had slightly less stems with moderate or worse die back (413 of 1269 v 1032 of 2503 stems; $\chi^2_{(df=1)} = 26.9$, $P<0.001$).

Table 3.4.15: Relationship between stem size, crown position and die back for all live hawthorn stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate (m) or severe/very severe die back (s); (iii) the number of larger stems that were fallen alive on ground (F) or were snapped/tipped and hung-up (S). The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Understorey				Ground			
Crown size: Gbh size-class (cm)	Large	Medium	Small	Very small	Large	Medium	Small	Very small
3-4.9	-	-	-	5	-	-	7	76 (10m,4s)
5-9.9	-	-	17	306 (21m,4s)	-	1 (1m)	288 (54m,7s)	259 (99m,49s)
10-14.9	-	-	71 (6m,1s)	316 (67m,27s)	-	35 (11m)	156 (77m,34s)	95 (17m,77s)
15-19.9	-	1	126 (29m)	164 (58m,54s)	-	45 (21m,1s)	80 (36m,40s)	26 (3m,23s)
20-24.9	-	8 (1m)	94 (24m3s)	49 (20m,23s)	1	20 (9m,4s)	13 (5m,8s)	6 (4s,2sF)
25-29.9	-	11	50 (15m,2s)	22 (8m,14s)	3 (2m)	9 (7m,2s)	4 (1m,3s)	-
30-34.9	-	13	26 (8m,4s)	4 (2m,1s,1sF)	2 (1m)	2 (1m,1mF)	2 (1s,1sF)	-
35-39.9	-	8	17 (7m,1s)	-	1 (1mF)	-	-	-
40-44.9	-	17	5 (2m,1s)	-	3 (1m,1mF)	2 (2sF)	-	-
45-49.9	1	10	2 (1m)	-	1 (1sF)	2 (1mF,1sF)	-	-
50-54.9	-	5	3 (1s,1sS)	-	-	-	1 (1sF)	-
55-59.9	-	6	-	-	-	-	-	-
60-69.9	3	1	-	-	-	-	-	-
70-79.9	1	-	-	-	-	-	-	-
80-94.9	2	1	-	-	-	-	-	-
All sizes	7	81	411	866	11	116	551	462
Die back								
% healthy/part	100	99	75	65	36	47	51	37
% moderate	-	1	22	20	45	45	31	28
% severe/very severe	-	-	3	15	9	8	18	34

Table 3.4.16: Relationship between stem size, crown position and die back for all live hazel stems ≥3cm gbh in the permanent transects in Monks Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate [(m)] or severe/very severe die back [(s)]; (iii) the number of larger stems that were fallen alive on ground [(F)] or were snapped/tipped and hung-up [(S)]. The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Understorey			Ground		
Crown size:	Medium	Small	Very small	Medium	Small	Very small
Gbh size-class (cm)						
3-4.9	-	-	15	-	15 (1m)	44 (19m,4s)
5-9.9	-	12 (1m)	277 (29m,11s)	2	123 (28m,2s)	68 (28m,28s)
10-14.9	-	125 (13m)	204 (55m,13s)	9 (4m)	28 (14m,8s)	9 (9s)
15-19.9	3	116 (18m,1s)	51 (22m,11s)	2 (1m)	3 (2m,1mF)	2 (1s,1sF)
20-24.9	6 (1m)	50 (15m,2s)	13 (4m,9s)	-	-	-
25-29.9	9 (4m)	25 (11m,2s)	6 (2m,3s,1sF)	-	-	1 (1s)
30-34.9	7	9 (4m,5s)	3 (3s)	-	1 (1s)	-
35-39.9	7 (1m)	9 (4m,2s)	2 (1s,1sF)	-	-	-
40-44.9	1 (2m)	1 (1s)	1 (1s)	-	-	-
45-49.9	1	2 (2s)	-	-	-	-
50-54.9	2 (2m)	1 (1m)	1 (1s)	-	-	-
55-59.9	-	-	1 (1s)	-	-	-
All sizes	38	350	574	13	170	124
Die back						
% healthy/part	76	77	70	62	67	27
% moderate	26	19	20	38	27	38
% severe/very severe	-	4	10	-	6	35

In addition, the canopy contained a small number of birch (mainly with very small crowns) and a single (medium-crowned) wild service tree. The sub-canopy also contained two goat willow and a birch (both with moderate die back), plus a single (healthy) wild service. The most numerous additional species in lower two layers were blackthorn (67 stems understorey, 43 ground), dogwood (27 understorey, 26 ground), and privet (66 ground).

3.4.2.4.2. Stem debarking

Debarking on the lower trunk of live stems in 1996 is shown in Table 3.4.17. This seemed to be mostly due to muntjac deer, but in a few cases it could have been where falling trees scarped stems. Almost 30% of stems were debarked. However, most damage was limited to one or a few small discrete patches to 1m up the stems: only 3% were classed as severely debarked. Midland hawthorn and hazel accounted for most of the debarked stems, but spindle, privet and dogwood had the highest percentage of debarked stems. Debarking was largely restricted to stems <20cm gbh and percentage damage increased progressively as stem size decreased. Severe debarking associated with stems <5cm gbh compared to larger stems (26 out 92 versus 76 out of 1023 stems; $\chi^2_{(df=1)} = 61.6$, $P<0.001$).

Table 3.4.17: Debarking damage on the lower trunk of live stems for each of the species in the permanent transects in Monks Wood in 1996. Excludes additional side forks and trunk shoots that divided below 1.3m height

	Number of stems					% of stems
	No debarking	Part-debarked	Moderately debarked	Severely debarked	Some debarking	Some debarking
Spindle	0	0	1	4	5	100
Privet	8	10	17	28	55	87
Dogwood	14	14	11	8	33	70
Hazel	677	272	126	26	424	39
Midland hawthorn	731	228	115	28	431	37
Common hawthorn	325	58	31	3	92	22
Blackthorn	67	12	5	0	17	20
Rose	19	0	1	2	3	14
Sallow	13	1	1	0	2	13
Ash	595	39	10	2	51	8
Elder	11	0	0	1	1	8
Field maple	321	1	0	0	1	0
Others	55	0	0	0	0	0
All species	2827	695	318	102	1115	28

3.4.2.5. Dead wood during 1985-96

3.4.2.5.1. Changes in snags

The basal area and density of snags was recorded in 1985 and 1996 (Table 3.4.18). Many species formed snags, but few contributed much to the total basal area and density. The main species involved was hazel, with field maple, ash, midland hawthorn and birch otherwise significant. Between 1985 and 1996 the snag basal area and density decreased by about 40%. Much of this was due to the reduction in hazel, field maple and birch snags, though nearly every other species declined. In both 1985 and 1996 most snags remained small and few attained >50cm gbh. Although the density of snags fell in almost all size-classes, the decline of those <10cm and 20-<30cm gbh was particularly severe.

Table 3.4.18: Change in the basal area, density and relative importance of snags in the permanent transects in Monks Wood between 1985 and 1996. Includes all dead standing stems ≥5cm gbh. Relative importance = [% total basal area + % all snags]÷2

	Basal area (m^2 ha^{-1})		Density (n ha^{-1})		Relative importance (%)	
	1985	1996	1985	1996	1985	1996
Hazel	1.5	0.7	482	307	49	47
Field maple	0.7	0.4	83	40	15	14
Ash	0.5	0.4	52	35	10	13
Midland hawthorn	0.2	0.1	133	94	10	12
Birch	0.5	0.2	15	6	8	5
Common hawthorn	0.1	<0.1	38	25	4	3
Blackthorn	0.1	<0.1	30	5	3	1
Oak	<0.1	0.1	1	3	1	3
Dogwood	<0.1	<0.1	1	5	<1	1
Elder	<0.1	<0.1	<1	2	<1	<1
Crab apple	<0.1	<0.1	<1	1	<1	<1
Privet	-	<0.1	-	<1	<1	<1
Goat willow	<0.1	-	<1	-	<1	-
Unidentified species	<0.1	-	2	-	<1	-
All species	3.6	2.1	839	523	100	100

Snags turnover was substantial during 1985-96 (Table 3.4.19). Only 14% of snags from 1985 remained standing in 1996, and only 22% of the snags present in 1996 had stood for over ten years. Percentage survival was: (i) slightly higher for snags of 30-<60cm gbh (17%) and least for snags of 5-<10cm gbh and ≥60cm gbh (both 12%); and (ii) highest for ash (25%), lower for hawthorn and hazel (12%), and least for aspen (2%) (including

Table 3.4.19: Fate, throughput and recruitment of snags in the permanent transects in Monks Wood between 1985 and 1996. The table shows the number of snags in each category, including all dead standing stems ≥5cm gbh; (a) includes live stems in 1985 that had died and collapsed by 1996; (b) includes live stems in 1985 that had died and which formed snags in 1996; and (c) includes stems <5cm gbh, <1.3m tall or not present in 1985 and which formed snags in 1996

	Snags in 1985	Fate of 1985 snags by 1996		Throughput 1985-96	Recruitment 1985-96	
		Still standing	Collapsed	(a)	(b)	(c)
Hazel	822	97	725	300	305	123
Midland hawthorn	227	35	192	198	122	5
Field maple	142	30	112	30	39	-
Ash	89	23	66	33	36	1
Common hawthorn	64	6	58	85	36	2
Blackthorn	52	1	51	41	7	-
Birch	25	5	20	7	5	-
Unidentified species	3	-	3	-		-
Oak	2	1	1	2	4	-
Dogwood	2	-	2	41	7	1
Crab apple	1	1	-	-	1	-
Elder	1	1	-	2	2	-
Sallow	1	-	1	6	-	-
Privet	-	-	-	7	-	3
Spindle	-	-	-	5	-	-
Guelder rose	-	-	-	3	-	-
Aspen	-	-	-	1	-	-
All species	1431	200	1231	761	564	135

species with >5 snags). Although 1325 live stems ≥ 5cm gbh died during 1985-96, 761 (57%) collapsed and failed to form snags in 1996. The percentage that did form snags was: (i) highest for stems of 30-<50cm gbh (71%) and least for stems of 5-<10cm gbh and ≥60cm gbh (34-39%); and (ii) highest for field maple, ash and hazel (50-57%), lower for hawthorn (38%), and least for dogwood and blackthorn (15%) (including species with >45 snags). In addition to the 200 snags that remained standing, another 335 recruited during the period, though 70% were <20cm gbh and only 12 exceeded 60cm gbh. A high proportion of the recruiting hazel snags had been <5cm gbh or <1.3m tall in 1985.

3.4.2.5.2. Fate of large logs, large collapsed snags, and large trees that died

The fate of fallen dead logs ≥25cm gbh plotted on the 1985 charts was examined, along with the fate of snags ≥45cm gbh that collapsed and trees ≥45cm gbh that died during

1985-96 (Table 3.4.20). Of the 127 larger logs in 1985, 99 (78%) had decayed away/were in small pieces by 1996. And of the 28 that survived, only 12 were classed as large logs (i.e. ≥45cm girth at the largest end and ≥2m in length). Survival rates were low for all species and for both small (25-50cm gbh) and large logs (80-<160cm, all of which were birch). Only five of the 12 large logs that persisted showed limited signs of decay, though these included all four of the large blackthorn logs. Of the 59 larger snags that collapsed, 35 persisted as large logs in 1996 but 24 did not. Amongst the species, hazel had only 30% of collapsed snags form large logs, whilst ash, birch and field maple achieved only 55-67%. Of the 68 larger live trees that died, 37 formed snags and 29 had collapsed and formed large logs by 1996, leaving two that formed neither. Amongst these, ash, birch, crab apple, hazel and oak moreover formed snags, whilst aspen, blackthorn and field maple moreover formed logs.

Table 3.4.20: Fate of large logs, large snags that collapsed and large trees that died between 1986 and 1996 as recorded in the permanent transects in Monks Wood. In addition the status in 1986 of the larger logs recorded in 1996 is shown. The values are the number in each category

	Fate of logs 1985-96[a]			Fate of large snags that collapsed during 1985-96[d]		Fate of large live stems that died during 1985-96[e]			Status in 1985 of large logs in 1996[b]		
	Large log in 1996[b]	Small log in 1996[c]	Gone/in small pieces in 1996	Formed large log in 1996[b]	Did not form large log in 1996	Formed snag in 1996	Formed large log in 1996[b]	Did not form large log in 1996	From logs in 1985	From snags in 1985[f]	From live trees in 1985[g]
Ash	2	3	29	8	4	16	9	-	2	8	32
Aspen	1	2	-	-	-	-	1	-	1	-	1
Birch	2	-	12	6	5	2	-	-	2	7	-
Blackthorn	4	7	12	1	-	-	3	-	4	-	4
Crab apple	-	-	-	-	-	2	-	-	-	-	-
Crack willow	-	-	-	-	-	-	-	-	-	-	1
Dogwood	-	-	1	-	-	-	-	-	-	-	-
Field maple	3	2	5	15	8	11	15	1	3	16	26
Hawthorn	-	2	9	1	-	-	-	-	-	1	5
Hazel	-	-	28	3	7	3	-	-	-	3	3
Oak	-	-	-	1	-	3	1	-	-	1	3
Goat willow	-	-	3	-	-	-	-	1	-	-	-
All species	12	16	99	35	24	37	29	2	12	36	75

[a] includes fallen dead stems ≥25cm gbh in 1985; [b] includes fallen dead stems ≥45cm girth at the largest end and ≥2m in length in 1996; [c] includes fallen dead stems smaller than criteria for large logs; [d] includes standing dead stems ≥45cm gbh in 1985; [e] includes live trees ≥45cm gbh in 1985; [f] includes tops off part-collapsed snags; [g] includes 11 ash, 3 field maple and 1 oak derived from branches or forks snapped out of live trees, which might have been dead standing beforehand

It was also possible to identify the status in 1985 of the 123 large fallen logs recorded in 1996 (Table 3.4.20). Most (75) were from live trees, though 15 of those involved were boughs snapped out of live trees and could have been dead standing in 1985. The remaining 48 had certainly been dead: 36 were recorded as snags and 12 as logs in 1985. Those from live trees were mainly solid or only part-rotten (68 out of 74), whereas those from snags were split equally between solid or part-rotten and rotten or very rotten, and those from logs were moreover either rotten or very rotten (7 out of 12).

3.4.2.5.3. Dead wood levels, dimensions and condition in 1996

The abundance, dimensions and condition of snags and fallen dead logs/branches was assessed in detail in 1996 (Table 3.4.21). The combined volume and length of these was $37m^3\ ha^{-1}$ and 5261m ha^{-1} respectively, much of which was on the ground. The individually measured large logs accounted for 37% of the volume and 12% of the length of all logs/branches, though these were sampled differently.

Most snags were <30cm gbh, <7m tall, had limited decay and/or most bark still present (Table 3.4.21). Much of the snag volume was split between field maple, ash and hazel, but hazel accounted for much of the length and density. This was because hazel snags were mainly short or medium height with a small gbh, whereas field maple and ash accounted for most of the tall, large gbh snags. In addition, birch and oak formed a few large snags.

Most fallen logs/branches were also <30cm girth at the point of intersection and had limited decay, but almost half had shed over half their bark (Table 3.4.21). Compared to snags, they were generally more decayed and retained less bark: 37 of 122 logs/branches were rotten or very rotten compared to only 10 of 892 snags ($\chi^2_{(df=1)} = 207.1$, $P<0.001$); and only 70 of 122 logs/branches retained 50% or more bark compared to 866 of 892 snags ($\chi^2_{(df=1)} = 238.3$, $P<0.001$). About 40% of the total volume and length of logs/branches was

Table 3.4.21: Quantity and condition of dead wood, including snags, large individually mapped logs and all fallen dead logs/branches as recorded in the permanent transects in Monks Wood in 1996. Cells show the number of snags/logs in each category unless stated otherwise

(a) Snags – based on measurements of snags ≥5cm gbh

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Height			Gbh			Decay state		Remaining bark	
				0-2.5m	3-7m	>7m	5-<30cm	30-<60cm	60-142cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Field maple	3.2	197	40	19	34	16	41	24	4	69	-	10	59
Ash	3.1	195	35	21	23	15	20	35	4	59	-	3	56
Hazel	2.9	923	307	237	279	7	473	50	-	514	9	9	514
Oak	1.8	23	3	-	3	2	1	2	2	5	-	1	4
Birch	0.8	26	6	2	7	1	4	2	4	9	1	-	10
Hawthorn	0.5	307	120	116	88	-	203	1	-	204	-	1	203
Crab apple	0.1	8	1	-	1	1	-	2	-	2	-	1	1
Blackthorn	<0.1	13	5	3	5	-	7	1	-	8	-	1	7
Dogwood	<0.1	14	5	3	5	-	8	-	-	8	-	-	8
Elder	<0.1	4	2	3	-	-	3	-	-	3	-	-	3
Privet	<0.1	1	1	1	-	-	1	-	-	1	-	-	1
All species	12.5	1712	523	405	445	42	761	117	14	882	10	26	866

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Table 3.4.21: continued

(b) All fallen logs/branches – based on line transect survey of fallen dead stems ≥15cm girth at point of intersection

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Girth at point of intersection			Decay state		Remaining bark	
			15-<30cm	30-<60cm	60-116cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Ash	9.6	1396	40	7	1	36	12	15	33
Field maple	3.7	698	20	4	-	16	8	8	16
Hazel	3.0	553	15	4	-	8	11	10	9
Blackthorn	2.9	262	5	3	1	7	2	3	6
Hawthorn	1.9	407	11	3	-	12	2	10	4
Oak	1.5	58	1	-	1	2	-	2	-
Birch	1.3	58	1	-	1	1	1	1	1
Aspen	1.0	58	1	-	1	2	-	1	1
Unidentified	0.2	58	2	-	-	1	1	2	-
All species	24.9	3549	96	21	5	85	37	52	70

(c) Large individually mapped logs – based on measurements of fallen logs ≥45cm girth at the largest end and ≥2m in length

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Girth at base			Length			Decay state	
				45-<75cm	75-<105cm	105-185cm	2-5m	6-10m	11-15m	Solid/part-rotten	Rotten/ very rotten
Field maple	3.2	147	26	36	7	2	25	18	2	34	11
Ash	3.2	156	25	33	8	1	16	20	6	34	8
Birch	1.0	16	5	3	4	2	9	-	-	-	9
Oak	0.7	19	2	1	2	1	1	2	1	4	-
Blackthorn	0.5	33	5	8	-	-	2	4	2	8	-
Hawthorn	0.2	17	4	6	-	-	3	3	-	6	-
Hazel	0.2	12	4	6	-	-	6	-	-	4	2
Aspen	0.1	8	1	2	-	-	-	2	-	1	1
Crack willow	<0.1	7	1	-	1	-	-	-	1	1	-
All species	9.2	414	72	95	22	6	62	49	12	92	31

ash, with blackthorn, field maple, hazel and hawthorn otherwise numerous. Only five logs measured ≥60cm girth at the point of intersection, including an ash, aspen, birch, blackthorn and oak. Unlike other species, the majority of hazel logs were well decayed.

Most of the individually measured large logs were 45-<75cm girth at the base, <10m long, and had limited signs of decay (Table 3.4.21). Much of the total volume and length was split between field maple and ash. Unlike other species, all birch logs were well decayed.

3.5. Stand change and natural disturbance at Langley Wood

3.5.1. Introduction

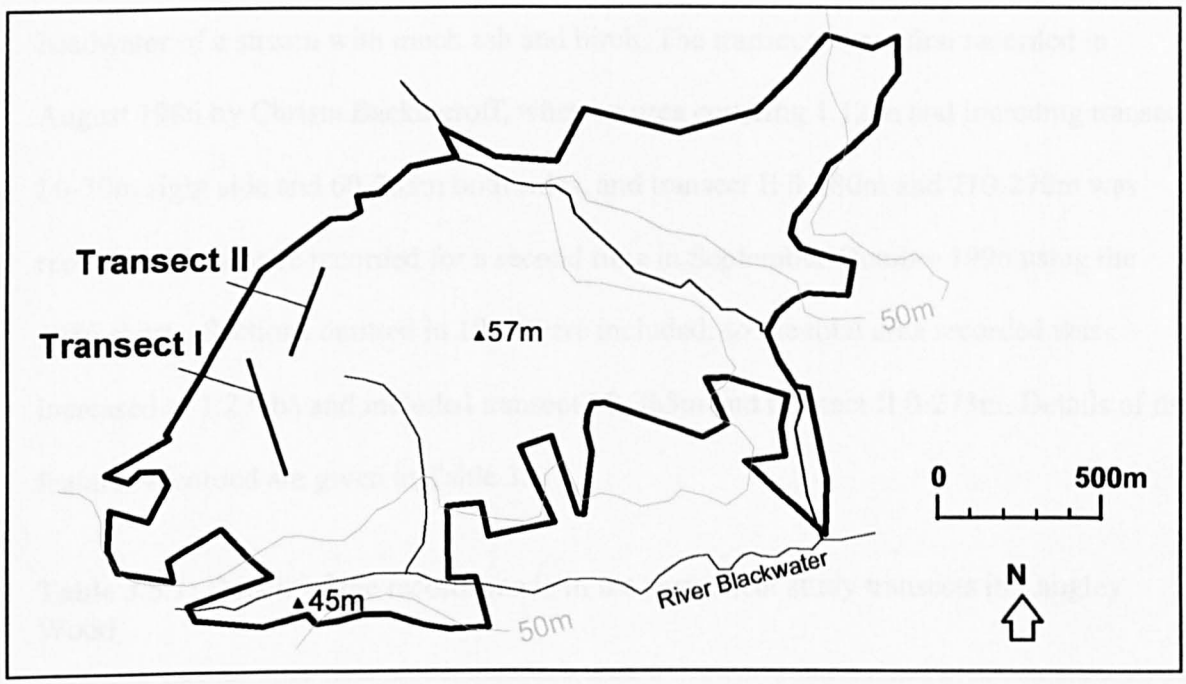
3.5.1.1. Site details

Langley Wood is located in Wiltshire, south England (see Figure 2.1, Table 2.1). It is described in detailed by Burton (2000). The wood is privately owned, but managed by English Nature under a National Nature Reserve agreement. It forms one of best and largest ancient oakwoods in lowland England, combining a large area of mature, semi-natural woodland, a wide variety of stand types, a rich flora/fauna (particularly vascular plants, bryophytes, epiphytes, invertebrates, birds) and many notable species. Bordering on The New Forest, it effectively forms an ungrazed version of the extensive ancient, wood pastures found here.

The reserve covers 218ha of gently undulating ground at 45m to 60m above sea level (Figure 3.5.1). London Clay underlies much of the site, but there are pockets of drift sand and gravel that create quite different soil conditions. The soils are mostly slowly permeable, moderately acidic, fine loamy and silty stagnogleys over clay, but some areas have well-drained, acidic, sandy, brown earth soils. Most of the woodland is mixed broad-leaved. Pedunculate oak, hazel and birch are generally widespread and abundant, whilst sessile oak, ash, small-leaved lime, alder, sweet chestnut and sycamore are only locally abundant (see Appendix for scientific names of species). Many minor species are present. In the ground vegetation, the most common species include bluebell and bramble, and (where soils are light and most acidic) bracken. Much of the vegetation corresponds to community W10 of the National Vegetation Classification (Rodwell 1991) and stand-types 6Db/c of Peterken (1993a).

The wood became part of the Royal Forest of Melchet about 1000 years ago, remaining outside the boundary of the New Forest. Beginning probably in the 14th century and

Figure 3.5.1: Langley Wood site map showing the extent and main features of the reserve and the location of the two permanent transects studied



continuing until the 19th century, the original wood-pasture was progressively enclosed to coppice as evidenced by numerous extant banks and ditches. Oak standards were maintained in both wood-pasture and coppice systems. Coppice management declined about 100 years ago and the site owner believes that the last coupes were cut about 1940. Thereafter, management was mainly limited to the removal of dead trees and fallen timber for firewood and maintenance of ditches and access rides, though a few blocks were clear-felled and converted to conifer plantations. Accordingly large areas of the wood have remained relatively undisturbed for many decades.

3.5.1.2. Recording

Details of the aims of recording and methodologies used are given in Section 2.4 and Table 2.3. Two, permanently marked, 20m wide transects were used for recording (see Figure 3.5.1). They were both located in areas treated as minimum-intervention. Transect I extended for 365m and mainly crossed stands of lime-birch-oak on relatively free-draining soils. However, it crossed a small valley with a stream at about 320m along. Transect II ran

for 273m and from about 45m along crossed stands mainly of oak-hazel on relatively free-draining soils. However, the first 45m included some particularly damp ground around the headwater of a stream with much ash and birch. The transects were first recorded in August 1986 by Christa Backmeroff, when an area covering 1.12ha and including transect I 0-30m right side and 60-365m both sides, and transect II 0-180m and 210-270m was recorded. They were recorded for a second time in September-October 1996 using the 1986 charts. Sections omitted in 1986 were included, so the total area recorded was increased to 1.276ha and included transect I 0-365m and transect II 0-273m. Details of the features recorded are given in Table 3.5.1.

Table 3.5.1: Details of the records made in the permanent study transects in Langley Wood

Date of recording	Features recorded
August 1986	• All individuals ≥1.3m height and all established seedlings, giving their location, species and status. • Gbh of all live and dead stems ≥5cm gbh, measured to the nearest cm. • Area covered by rhododendron. • Position of various larger fallen dead logs (criteria not specified), often with a gbh measurement for the largest end and indication of the species. • Various salient features. • Most records were drawn onto a set of A4 scale charts, each covering a 30m long transect section.
September-October 1996	• All individuals ≥1.3m height and all established seedlings, giving their location and status. • Gbh of all live stems ≥3cm gbh and all dead stems ≥5cm gbh, to the nearest half cm. • Area covered by rhododendron. • Condition of most live stems, including descriptive notes and allocation of crown position, crown size, crown die back, and scoring of debarking by grey squirrels, and cause of demise for stems that had been lost. • Snag height and description of decay state, and condition of logs plotted in 1986. • Fallen dead wood abundance and condition – this was done using twenty-one, 20m long line transects, positioned every 30m across the middle of the transects, and by measuring the girth or diameter (to nearest cm) of all fallen dead stems ≥15cm girth where they crossed the lines – in addition, all fallen dead logs within the transects that were ≥30cm girth at their largest end and ≥1m length were mapped and measured, taking the length (to the nearest 0.1m) and girth at each end (to nearest cm) – the origin and condition of all recorded pieces was noted. • Extent of canopy gaps and notes on their origin and understorey infilling. • Various salient features.

3.5.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. Firstly, the analysis focused on the general changes in stand composition and structure since the last major felling up to 1986, based on an assessment of the stand characteristics when the transects were first recorded. A more detailed analysis of stand changes during 1986-96 was made by comparing the features recorded at both dates and by an assessment of the additional features recorded in 1996. The transects were combined for the general analyses of the stands, but they were partitioned into three areas for more detailed examination based on major differences in composition. As appropriate, either the 1.12ha recorded in both 1986 and 1996 or the 1.276ha recorded only in 1996 were included in the analysis.

The data set provided information on 5814 stems/individuals/seedlings/logs. A small number of mistakes and apparent errors were corrected for and various assumptions were made. The main problem was with stem relocation and gbh measurement on complex, multi-stemmed and forked hazels. In addition, various additional trunk shoots and side forks appeared to have been omitted in 1986. Various standard measures were calculated, with annual rates of change being based on ten growing seasons, and stems <5cm gbh recorded in 1986 being scored as 3cm gbh for basal area calculations.

3.5.2. Results

3.5.2.1. Stand development before 1986

The study transects were located in an area that appeared to been cut over around 1940 leaving some standard trees. It was then allowed to naturally regenerate and left largely untreated thereafter. In 1986 it was dominated by dense, high forest, with 16 tree and shrub species were present and a basal area around $33m^2\ ha^{-1}$ (Table 3.5.1). The overstorey was mainly birch, lime and oak, and the understorey mainly hazel and hawthorn.

Table 3.5.1: Basal area, density and size-class distribution for live individuals/stems recorded on the two permanent transects in Langley Wood in 1986. Includes all individuals ≥1.3m height and all recorded stems. nr = not recorded

		Basal area (m^2 ha^{-1})	Individuals (n ha^{-1})	Stems (n ha^{-1})	Gbh size-class (cm) (n stems)										
					<10	10-<20	20-<40	40-<60	60-<80	80-<100	100-<150	150-<200	200-<250	250-<350	All sizes
Major trees	Oak	18.4	69	69	-	-	-	1	6	3	14	27	19	7	77
	Birch	6.8	355	400	24	96	150	87	61	13	13	2	-	-	448
	Lime	5.3	76	504	23	125	265	101	45	7	1	-	-	-	565
Minor trees	Ash	0.3	354	371	325	84	4	1	-	1	-	-	-	-	415
	Beech	<0.1	13	14	3	5	7	1	-	-	-	-	-	-	16
	Sweet chestnut	<0.1	4	4	-	-	2	1	1	-	-	-	-	-	4
	Sycamore	<0.1	3	3	-	2	1	-	-	-	-	-	-	-	3
	Alder	<0.1	1	1	-	-	-	-	-	1	-	-	-	-	1
Major shrubs	Hazel	0.7	321	1228	1030	326	19	-	-	-	-	-	-	-	1375
	Hawthorn	0.6	90	133	44	36	56	13	-	-	-	-	-	-	149
Others	Yew	0.1	1	3	-	-	-	1	1	-	1	-	-	-	3
	Field maple	<0.1	6	6	-	-	2	5	-	-	-	-	-	-	7
	Blackthorn	<0.1	6	6	6	1	-	-	-	-	-	-	-	-	7
	Willow	<0.1	3	3	-	-	2	-	1	-	-	-	-	-	3
	Crab apple	<0.1	2	3	-	1	1	-	1	-	-	-	-	-	3
	Rhododendron	<0.1	1	nr	-	-	-	-	-	-	-	-	-	-	n.r.
	All species	32.7	1304	2746	1455	676	509	211	116	25	29	29	19	7	3076

The stand comprised a mixture of coppice and maiden growth, with a few ex-standards and other retained trees. Coppice individuals (which had several or many stems) were mainly of hazel and lime, but with some hawthorn and other species too. The coppice hazel included a few stools with many live stems (up to 39), but most had less than ten. Most recorded lime were coppice individuals and most of these were multi-stemmed, including about 40% with at least ten live stems and one with nearly 30 live stems. They were grouped (see Figure 3.5.2) and in several cases it was difficult to decide which were separate individuals: some might have been fragments of the same individual. Maidens (most of which were single-stemmed) included many birch and ash and a few lime (which were located close to lime coppice stools) (see Figure 3.5.2). A scatter of medium-large oaks were recorded (Table 3.5.1, Figure 3.5.3), most of which must have been standards retained during the last fellings. In addition, a large yew (end transect II) and perhaps some of the large birch had also been retained. Including all the oaks ≥100cm gbh and the large yew, the density of retained trees was 61ha^{-1}. Many minor trees and shrubs were recorded, including a few or several alder, beech (mainly single-stemmed, maidens), blackthorn, crab apple, field maple, rhododendron, sweet chestnut (maidens), sycamore (maidens), and willow (sizes for each are given in Table 3.5.1).

The distribution of the main species differed considerably along the transects (Figures 3.5.2-3). In particular: (i) lime occurred only on transect I and mainly in three groups at 60-160m, 200-285m, and 340m to the end; (ii) birch occurred mainly along transect I, where lime was lacking and between oak standards, on the damper ground near the start and in a few patches along the rest of transect II; (iii) most ash and the willow were also found on damp ground at the start of transect II, whilst the single, well-grown alder was recorded near the stream on transect I; (iv) hazel and hawthorn occurred mainly on the drier ground on transect II in between oak standards, but also in parts of transect I away from lime and the ground around the stream where downy birch, oak and bracken predominated; and (v)

Figure 3.5.2: Distribution of birch, lime and ash individuals recorded on the two permanent transects in Langley Wood in 1986. Each transect is shown in two strips: transect 1 on the left and transect 2 on the right. Symbols show the location, species, size of birch (multi-stemmed individuals are based on the largest stem), and origin of lime individuals. Those in transect 1 from 0-30m (left side) and 30-60m along and transect 2 from 180-210m and 270-273m along are based on records from 1996. Includes all individuals alive and ≥1.3m tall

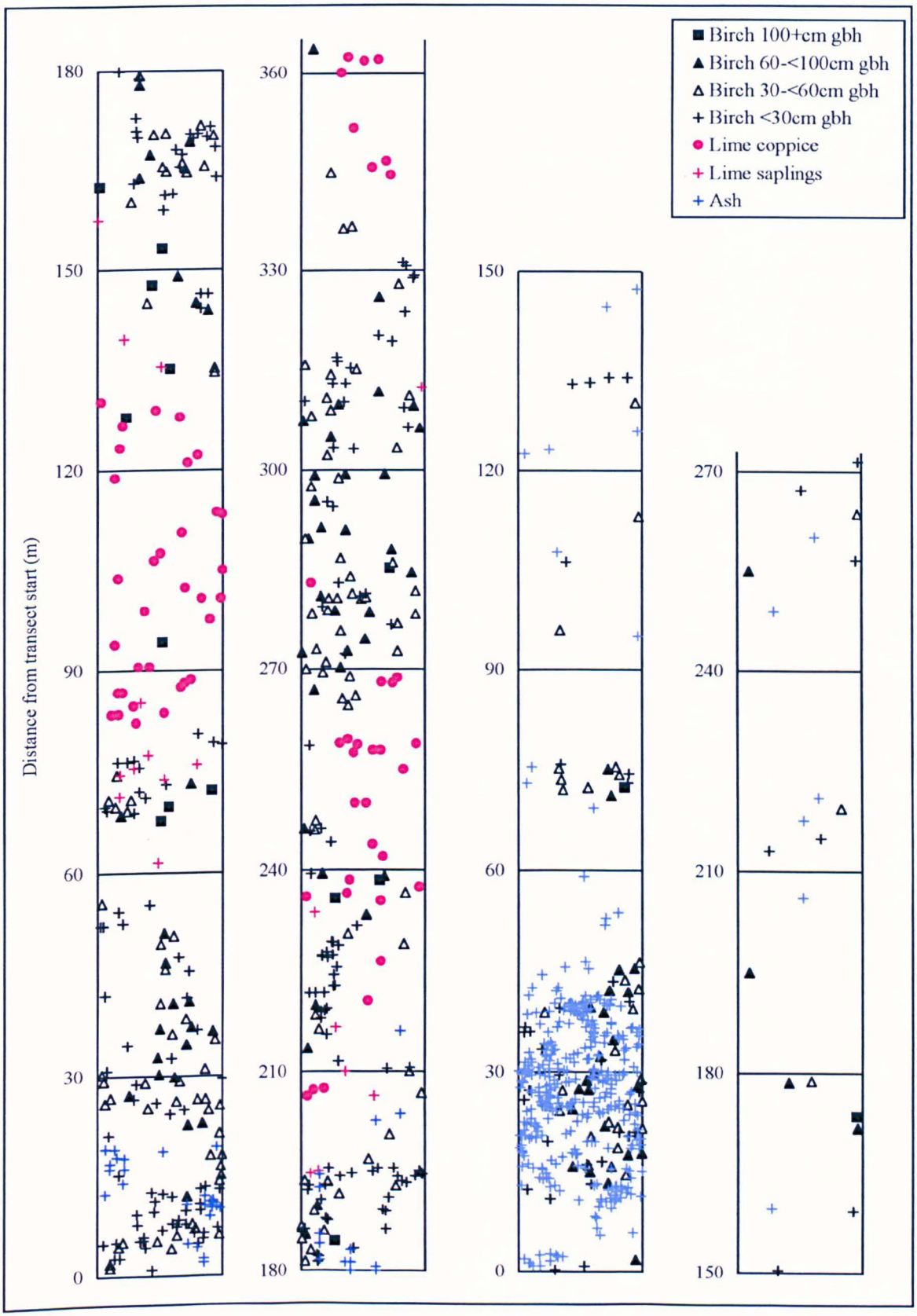
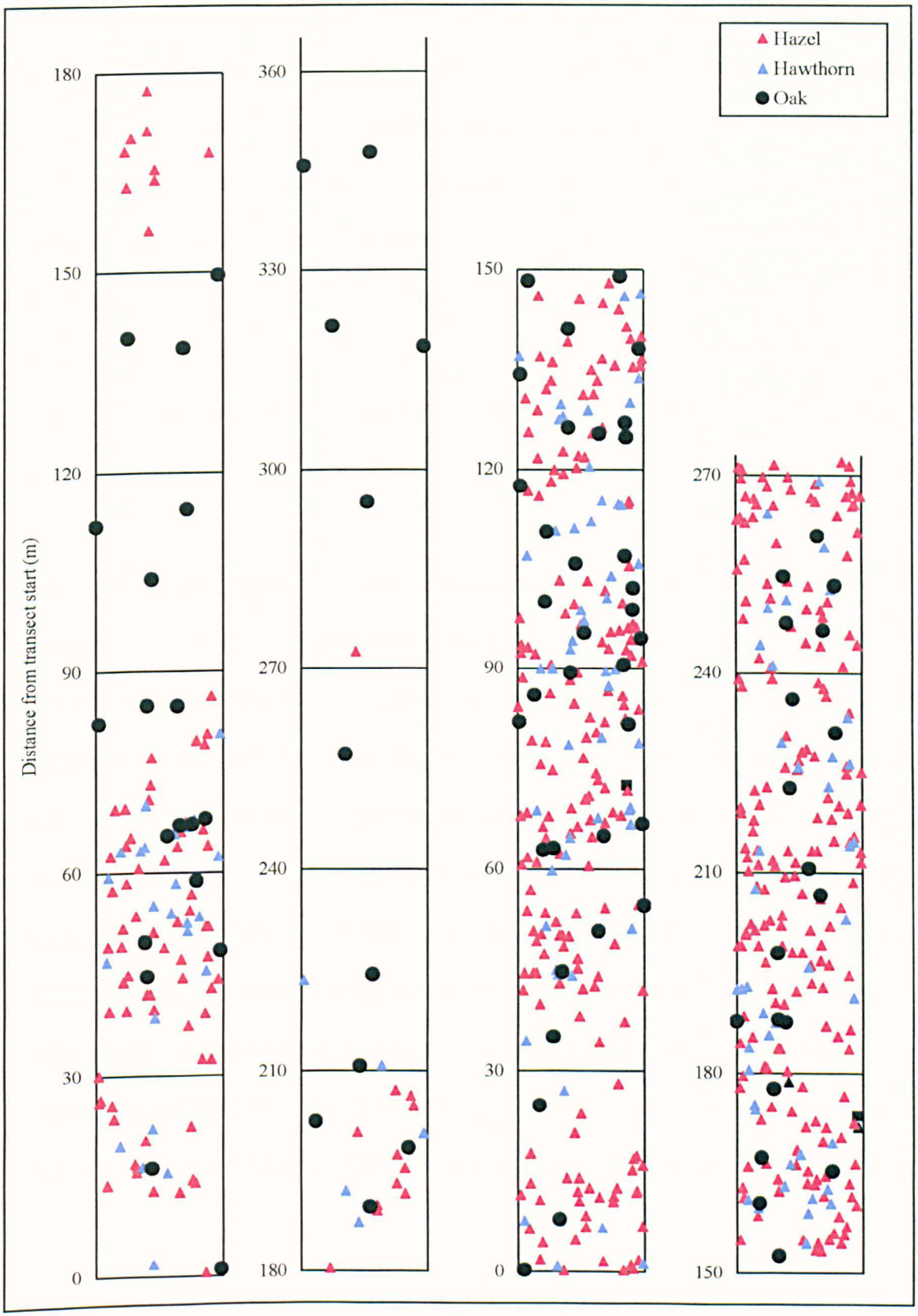


Figure 3.5.3: Distribution of oak, hazel and hawthorn individuals recorded on the two permanent transects in Langley Wood in 1986. Symbols show the location and species of each individual. Those in transect 1 from 0-30m (left side) and 30-60m along and transect 2 from 180-210m and 270-273m along are based on records from 1996. Includes all individuals alive and ≥1.3m tall



blackthorn, crab apple, field maple and most beech were found on the drier ground on transect II, whilst the sycamore occurred further down transect I.

Most of the 265 snags recorded were small, with all but three <45cm gbh. For the most part, these had probably been excluded and left no canopy gaps. However, some larger snags and fallen dead trees were recorded. These included: (i) a 118cm gbh oak snag and a 117cm gbh fallen oak that appeared to have been excluded by larger adjacent oaks; (ii) three groups of windthrown/snapped trees (mainly birch) on transect II including, four 55-82cm gbh birch in section two, four 50-68cm gbh birch plus a live 41cm gbh uprooted live birch in section 3, and two 40-76cm gbh birch plus a 134cm oak in section 6; and (iii) two other isolated windthrown birch sized 70-72cm gbh. Possibly the birch had been weakened by the 1976 drought.

The predominately right-skewed size-distribution of the surviving live stems (Table 3.5.1) reinforced the view that competitive exclusion had been a major process during the preceding decades. Most remaining trees were either oaks retained at the last felling or other individuals that had established soon after and self-thinned over many decades to leave: (i) a few, dominant, fast-growing, large-size stems of mainly birch and lime; and (ii) many suppressed, slower-growing, small-medium stems of many species. However, there was a surprisingly large number of small ash and hazel stems (Table 3.5.1), indicative of some recent regeneration. Although many small hazel stems were on existing stools, a few represented newly established individuals. Many of the small ash were suppressed saplings, growing on the damp ground on transect II below a canopy of birch: the site owner suggested they had invaded following the death of a large canopy tree around 1960.

3.5.2.2. General aspects of stand change during 1986-96

3.5.2.2.1. Canopy gaps

Changes within the two transects were largely the result of natural processes within closed stands. However, some canopy gaps had developed by 1986 and by 1996 gaps covered 12% of the two transects. These were mostly infrequent and small-sized, but on parts of transect II they were more extensive and four sections had 20-40% gaps (Figure 3.5.4). Many of the gaps were small, narrow and/or filled below by understorey growth, and none permitted an extensive influx of light to reach the woodland floor. They were mainly produced by the fall/windthrow of birch or the loss of large oak boughs. Moreover, birch windthrow was associated with all sections that had >20% gaps.

3.5.2.2.2. Changes in stem basal area and density of live stems/individuals

Changes in the basal area and density of live stems/individuals over 1986-96 were determined separately for: (i) the lime-birch-oak stands along transect I; (ii) the oak-hazel stands from 45-270m along transect II; and (iii) the ash-birch-oak stands from 0-45m along transect II. Only sections recorded at both dates were included.

For the lime-birch-oak stands on transect I (Table 3.5.2), the basal area of live stems increased on average by 0.47m^2 ha^{-1} per year to almost 37m^2 ha^{-1} and by 15% overall. Each of the ten 600m^2 transect sections also increased in basal area, with the average increasingly significantly from 33.1 to 38.1m^2 ha^{-1} (paired-sample test: $t_{(df=9)} = 12.6$, $P<0.001$). In contrast, the density of live individuals and stems over 1986-96 dropped by 17-22%. Stem density also fell in all of the ten sections, with the average declining significantly from 1735 to 1435ha^{-1} (paired-sample test: $t_{(df=9)} = 7.0$, $P<0.001$). Lime remained the most important species, birch and oak declined in importance but remained second and third respectively, and hazel increased but remained fourth. Lime retained the second greatest share of and increased in basal area. It also remained at around half of

Figure 3.5.4: Location of canopy gaps along the two permanent transects in Langley Wood in 1996. The transect number is shown at the bottom and the distance along to the right. The area occupied by gaps in each in 600m^2 section is shown to the left as a percentage

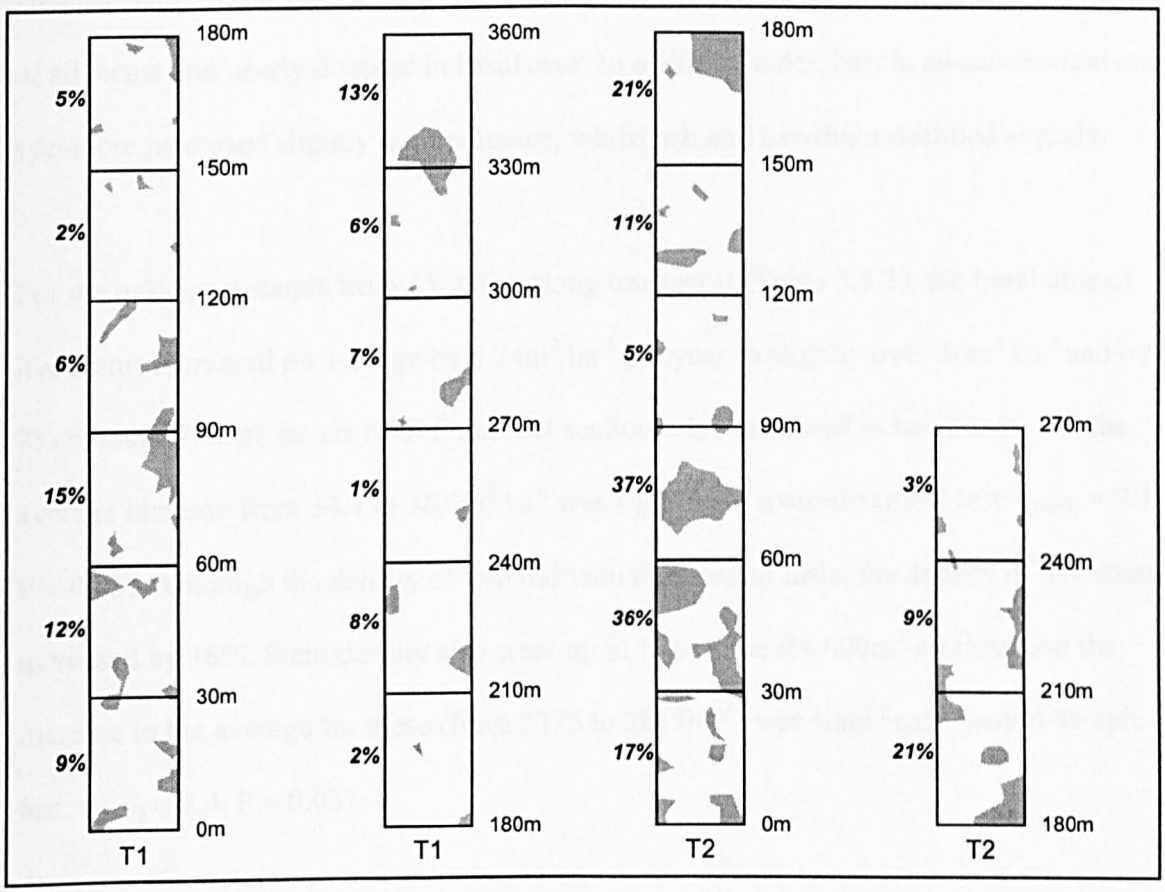


Table 3.5.2: Change in the basal area, density and relative importance of live stems/individuals recorded along transect I in Langley Wood between 1986 and 1996. Includes individuals ≥1.3m height and stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})		Individuals (n ha^{-1})		Stems (n ha^{-1})		Relative importance (%)	
	1986	1996	1986	1996	1986	1996	1986	1996
Lime	9.4	11.5	133	128	869	700	40	40
Birch	9.0	10.0	466	330	520	361	29	26
Oak	13.0	14.2	45	44	45	44	22	21
Hazel	0.2	0.4	72	73	216	270	7	10
Hawthorn	0.1	0.1	27	25	19	13	1	1
Ash	<0.1	<0.1	66	25	39	25	1	1
Alder	0.1	0.2	2	2	2	2	<1	<1
Sweet chestnut	<0.1	0.2	3	3	3	3	<1	<1
Sycamore	<0.1	<0.1	5	5	5	5	<1	<1
Beech	<0.1	<0.1	5	3	5	5	<1	<1
All	32.0	36.7	822	638	1722	1427	100	100

all stems. Birch increased in basal area (but declined in its overall share), whilst its stem density fell. Oak accounted for few individuals, but all were large, and it retained the greatest share of the basal area. Amongst the other species, hazel increased from 13 to 19% of all stems and nearly doubled in basal area. In addition, alder, beech, sweet chestnut and sycamore increased slightly in importance, whilst ash and hawthorn declined slightly.

For the oak-hazel stands from 45-270m along transect II (Table 3.5.3), the basal area of live stems increased on average by $0.24m^2\ ha^{-1}$ per year to slightly over $36m^2\ ha^{-1}$ and by 7% overall. Five of the six $600m^2$ transect sections also increased in basal area, and the average increase from 34.4 to $36.6m^2\ ha^{-1}$ was significant (paired-sample test: $t_{(df=9)} = 2.1$, $P = 0.05$). Although the density of live individuals changed little, the density of live stems increased by 18%. Stem density also went up in five of the six $600m^2$ sections and the increase in the average for these (from 2375 to $2817ha^{-1}$) was significant (paired-sample test: $t_{(df=9)} = 2.4$, $P = 0.03$).

Oak was the most important species in 1986, but it was replaced by hazel in 1996. Hawthorn and birch remained in third and fourth positions. Oak was represented by a small number of large trees, which increased in and retained by far the greatest share of the basal area. On the other hand, hazel was represented by many small stems: it doubled in basal area but accounted for only 4-8% of the total, and increased by almost a third in stem density. Hawthorn changed little, but birch declined in importance because both its basal area and stem density dropped substantially. Other species changed little in importance, though there were notable percentage increases in the basal area of ash, beech, blackthorn and sweet chestnut, and blackthorn made a notable increase in density.

For the ash-birch-oak stands from 0-45m along transect II (Table 3.5.4), the basal area of live stems remained virtually unchanged, whilst the density of live individuals/stems fell

Table 3.5.3: Change in the basal area, density and relative importance of live stems/individuals recorded from 45-270m along transect II in Langley Wood between 1986 and 1996. Includes individuals ≥1.3m height and stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})		Individuals (n ha^{-1})		Stems (n ha^{-1})		Relative importance (%)	
	1986	1996	1986	1996	1986	1996	1986	1996
Oak	28.0	29.5	110	97	110	97	44%	43%
Hazel	1.4	2.8	677	718	1831	2367	40%	45%
Hawthorn	1.3	1.3	195	246	254	244	7%	6%
Birch	2.0	1.1	100	41	105	46	5%	2%
Ash	0.2	0.4	56	31	41	33	1%	1%
Yew	0.3	0.4	3	3	8	8	<1%	<1%
Field maple	0.2	0.3	18	18	18	18	<1%	<1%
Beech	0.1	0.2	28	21	26	21	<1%	<1%
Crab apple	0.1	0.2	5	5	8	8	<1%	<1%
Blackthorn	<0.1	<0.1	18	36	10	15	<1%	<1%
Sweet chestnut	<0.1	<0.1	3	3	3	3	<1%	<1%
Rhododendron	n.r	n.r	3	3	n.r	n.r	<1%	<1%
All	33.8	36.2	1215	1221	2413	2859	100%	100%

Table 3.5.4: Change in the basal area, density and relative importance of live stems/individuals recorded from 0-45m along transect II in Langley Wood between 1986 and 1996. Includes individuals ≥1.3m height and stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})		Individuals (n ha^{-1})		Stems (n ha^{-1})		Relative importance (%)	
	1986	1996	1986	1996	1986	1996	1986	1996
Ash	1.9	3.5	3900	2122	3122	2122	32%	31%
Birch	12.6	10.6	800	544	811	544	27%	23%
Oak	15.0	14.4	56	44	56	44	24%	23%
Hazel	0.7	1.4	1556	1378	1200	1378	12%	19%
Hawthorn	0.8	0.8	133	67	111	67	2%	2%
Willow	0.7	0.8	33	22	33	22	1%	2%
Sweet chestnut	<0.1	0.3	11	11	11	11	<1%	<1%
Beech	<0.1	<0.1	11	11	11	11	<1%	<1%
Holly	-	<0.1	-	11	-	11	<1%	<1%
All	31.8	31.7	6500	4211	5344	4211	100%	100%

by 21-35%. Overall, the importance of the four main species remained as ash> birch> oak>hazel, though hazel showed a marked increase in importance whilst the other three species all declined slightly. Ash and hazel were both represented by many small stems: they both increased substantially in basal area, but ash declined in stem density whilst

hazel increased. Birch had the second highest basal area, though both this and birch stem density fell markedly. Oak included just five large trees, one of which died, but it still retained 45-47% of the total basal area. The other minor species changed little in importance, though sweet chestnut doubled in basal area, and holly recruited.

3.5.2.2.3. Survival, mortality and recruitment patterns

The change in basal area and density of live individuals/stems was related to the survival, mortality and recruitment of stems. The fate and recruitment of live stems during 1986-96 is shown in Table 3.5.5. Of the 3071 live stems recorded in 1986, 73% remained alive in 1996. The overall mortality rate was 3.12% a^{-1}. Stems <5cm gbh in 1986 had by far the highest mortality rate, whilst stems ≥40-<160cm gbh had lower rates, and all stems ≥160cm gbh survived (Table 3.5.6). A small number of losses, mostly ash, hazel and hawthorn, were reduced to alive below 1.3m in height. Of those that died, 26% were still standing and formed snags in 1996. Stem loss was moderated because 224 stems recruited (i.e. they grew to or over the 5cm gbh recording threshold), most of which were on existing hazel individuals: in some cases it was difficult to decide if these were 'real' recruits or had simply been omitted in 1986. However, slightly over one hundred new individuals managed to establish, mainly blackthorn, hawthorn or hazel.

Survival, mortality and recruitment patterns differed among the species (Tables 3.5.5-6). Ash mortality was high because so many of the population were small-sized: overall 96% of the ash lost were <10cm gbh and none over 20cm gbh died. Excluding stems <10gbh, the mortality rate for ash was only 0.93% a^{-1}, similar to that of oak (0.95% a^{-1}) and less than lime or birch (2.0-3.8% a^{-1}) of the same size. Although only 17% of the stems that died formed snags in 1996, most still appeared to have been excluded, sometimes after having been knocked over by falling trees or canopy debris.

Table 3.5.5: Fate and recruitment of live stems/individuals on the two permanent transects in Langley Wood between 1986 and 1996. The table shows the number of stems recorded in each category and the annual mortality rate (m). The number of fallen live stems in 1986 that survived is shown in superscript brackets in column five. Includes all live stems in 1986

		1986	1986-1996							
			Fate of 1986 stems by 1996					m rate	Recruits	
		Live stems	Standing alive	Fallen alive	Alive below 1.3m only	Died (snag)	Died (fallen)	% a^{-1}	Stems grown to ≥5cm	New individuals
Major trees	Ash	415	221	-	24	9	161	6.1	1	-
	Birch	448	295	3	1	40	105	4.0	-	-
	Lime	565	442	6	-	36	81	2.3	-	-
	Oak	77	70	-	-	3	4	0.9	-	-
Major shrubs	Hawthorn	149	113	$5^{(3)}$	8	10	18	2.7	6	43
	Hazel	1370	1048	$17^{(2)}$	16	66	240	2.6	212	58
Other species	Blackthorn	7	3	1	-	1	3	8.1	4	11
	Willow	3	2	-	-	-	1	4.0	-	-
	Beech	16	12	-	1	1	2	2.8	-	-
	Field maple	7	7	-	-	-	-	zero	-	-
	Sweet chestnut	4	4	-	-	-	-	zero	-	-
	Sycamore	3	3	-	-	-	-	zero	-	-
	Yew	3	3	-	-	-	-	zero	-	-
	Crab apple	3	2	$1^{(1)}$	-	-	-	zero	-	-
	Alder	1	1	-	-	-	-	zero	-	-
	Rhododendron	[1 bush]	[1 bush]	-	-	-	-	zero	-	-
	Holly	-	-	-	-	-	-	-	1	1
	All species	3071	2236		50	166	615	3.1	224	113

Table 3.5.6: Mortality rate (m % a^{-1}) for stems of different sizes on the two permanent transects in Langley Wood between 1986 and 1996. Includes all live stems recorded in 1986. Some size-classes were not represented (-) and in some classes all stems died

Gbh size-class (cm)	Ash	Birch	Lime	Oak	Hazel	Hawthorn	All species
<5	31.88	all	all	-	5.58	4.32	7.40
5-<10	5.13	8.96	9.78	-	1.86	4.59	2.89
10-<20	1.00	7.72	6.19	-	1.04	1.17	2.65
20-<40	0.00	4.20	1.59	-	3.01	2.84	2.50
40-<60	0.00	2.29	0.10	0.00	-	1.66	1.04
60-<80	-	1.77	0.00	10.40	-	-	1.28
80-<100	0.00	0.00	0.00	0.00	-	-	0.00
100-<120	-	1.17	-	2.21	-	-	1.42
120-<140	-	0.00	0.00	3.97	-	-	1.33
140-<160	-	-	-	0.87	-	-	0.87
160-<350	-	0.00	-	0.00	-	-	0.00

Birch mortality was high in the smaller size-class up to about 40cm gbh, but some larger trees up to 102cm gbh also died. Most mortality, particularly amongst the smaller stems, was accredited to exclusion. The general effect was a thinning of existing dense birch groups. However 27 of the larger trees that died appeared to have died after being wind-damaged (Table 3.5.7): seven were already on the ground, tipped or snapped in 1986, but 20 were damaged after 1986 and had died by 1996. These accounted for 24 of the 33 stems >35cm gbh that died. In addition, eight other wind-damaged birch remained alive in 1996, including three uprooted, two tipped and three crown-snapped trees. Much of the wind damage occurred along transect II, in sections 1-3 and 6, expanding the areas of wind damage present in 1986 and creating some sizeable gaps (Figure 3.5.4). Only about a quarter of losses formed snags in 1996, though proportionally more of the larger losses remained standing.

Exclusion was the main cause of death for lime: most losses were small; mortality rates increased as stem size decreased; and virtually all stems above 40cm gbh survived. However, a single lime stem at 39cm gbh at the end of transect I was cut down when the adjacent conifer stand was felled. Many multi-stemmed lime individuals thinned out and

Table 3.5.7: Birch stems that died due to wind damage between 1986 and 1996 or survived but were baldy wind-damaged on the two permanent transects in Langley Wood. The table shows the size of stems affected. Stems with a question mark were only possible wind-damaged losses. Some snapped snags in 1996 might also have been wind-damaged losses

Fate	Stem gbh in 1986 (cm)	Damage
Died 1986-96	59, 59, 41, 38, 31, 27, 25	Already blown over, tipped or snapped by wind in 1986
	102, 76?, 72, 72, 68, 67, 67?, 66, 64, 60?, 59, 54, 52, 49, 44?, 42, 40?, 40?, 39, 38?	Blown over, tipped or snapped off by wind and died after 1986
Damaged 1986-96	60, 38, 35	Blown over after 1986 but still alive on ground in 1996
	137, 70	Tipped after 1986 but still alive on lean in 1996
	89, 62, 53	Much of crown blown out after 1986 but still alive in 1996

the percentage of single-stemmed individuals increased from 8 to 34%. Although 117 stems died, only four individuals died off completely. About a third of the lime lost formed snags in 1996 and proportionally more of the larger stems remained standing.

Oak mortality was low. It included two trees of 126-157cm gbh and five at 64-107m gbh. The latter were excluded, whilst the 126cm gbh tree failed in the canopy and the 157cm gbh tree was windthrown and left a gap. Three of the trees remained as snags in 1996.

The two main understorey species, hazel and hawthorn, had similar moderate rates of mortality. Although hazel stems of all sizes died, rates were highest for the very smallest and largest stems. Hazel losses mainly resulted in the thinning of multi-stemmed individuals: 322 stems were lost but only 39 individuals died completely. Most hazel mortality was accredited to exclusion, but falling canopy debris and windthrown trees damaged some stems. Only a quarter of stems lost persisted as snags and the proportion that collapsed was high for stems <5cm gbh. Recruitment of new hazel stems was substantial, and these helped keep the number of stems sized 5-<10cm gbh high (from 620 to 514). Although many new stems were on existing individuals, 58 new hazel bushes formed. Recruiting stems were particularly numerous along transect II (Table 3.5.8), where the canopy was more broken and formed mainly of oak with some birch. New individuals

Table 3.5.8: Distribution of recruiting stems (grew to ≥5cm gbh) and (in brackets) individuals (grew to ≥1.3m height) between 1986 and 1996 on the two permanent transects in Langley Wood. The table shows the number of stems/individuals in each transect section

Transect section	Hazel	Hawthorn	Black-thorn	Ash	Holly	All new stems	All new individ-uals
1:1 right side	6 (3)	- (3)	-	-	-	6	6
1:3 both sides	6 (2)	-	-	-	-	6	2
1:4 both sides	-	-	-	-	-	-	-
1:5 both sides	-	- (1)	-	-	-	-	1
1:6 both sides	7 (1)	- (1)	-	-	-	7	2
1:7 both sides	7 -	-	-	-	-	7	-
1:8 both sides	- (1)	-	-	-	-	-	1
1:9 both sides	-	-	-	-	-	-	-
1:10 both sides	-	-	-	-	-	-	-
1:11 both sides	-	-	-	-	-	-	-
1:12 both sides	-	-	-	-	-	-	-
2:1 both sides	13 (2)	- (3)	-	-	1 (1)	14	6
2:2 both sides	20 (5)	- (5)	4 (9)	1 (-)	-	25	19
2:3 both sides	50 (19)	5 (19)	- (2)	-	-	55	40
2:4 both sides	20 (7)	1 (1)	-	-	-	21	8
2:5 both sides	19 (7)	- (2)	-	-	-	19	9
2:6 both sides	19 (3)	- (2)	-	-	-	19	5
2:8 both sides	21 (3)	- (2)	-	-	-	21	5
2:9 both sides	24 (5)	- (4)	-	-	-	24	9
All sections	212 (58)	6 (43)	4 (11)	1 (-)	1 (1)	224	113

were located mainly in sections 1-3 on transect I and along transect II, where hazel was already numerous in 1986.

Hawthorn stems of all sizes died, though mortality rates were highest for stems <10cm gbh. Although only 36 stems were lost, 23 hawthorns individuals died. Most losses were due to exclusion, though falling trees or boughs hit some stems first. Half of the stems that died remained standing as snags in 1996. Recruitment of new hawthorn stems was low but 43 new hawthorn bushes form and these were particularly numerous along transect II and especially in section 3 (Table 3.5.8), which had a large canopy gap by 1996.

Most minor species changed little. All alder, crab apple, field maple, rhododendron, sweet chestnut, sycamore and yew stems survived and no recruits formed. Only the smallest of

the three willow individuals died. Beech, however, lost four of 16 individuals: no trace was found of the smallest at 3cm gbh, but the others at 10, 29 and 34cm gbh were all destroyed by squirrel debarking. Blackthorn had a high turnover of individuals: 4 out the 7 present in 1986 died, but 11 new individuals recruited nearby from suckers. In addition, a single holly recruited, albeit this was pinned under an oak branch and part-grazed by deer.

3.5.2.2.4. Established seedlings

Table 3.5.9: Number and distribution of established seedlings/bushes (several years old and ≥ 30cm height) along the two permanent transects in Langley Wood in 1996. The table shows the number of individuals in each transect section. Excludes individuals that were recorded as alive >1.3m height in 1986, though not all sections were recorded in 1986

Transect section	Haw-thorn	Hazel	Holly	Black-thorn	Ash	Horn-beam	Other species*	Total
1.1	89	53	6	-	17	6	-	171
1.2	83	20	36	43	5	13	-	200
1.3	12	5	19	-	-	1	-	37
1.4	-	-	34	-	-	-	-	34
1.5	3	3	11	-	-	-	-	17
1.6	4	-	1	-	2	-	-	7
1.7	1	3	2	-	-	-	-	6
1.8	1	-	4	-	-	-	1	6
1.9	-	-	1	-	-	-	-	1
1.10	-	-	1	-	-	-	-	1
1.11	-	-	3	-	-	-	-	3
1.12	-	-	2	-	-	-	-	2
2.1	48	10	6	-	11	-	-	75
2.2	34	10	4	19	2	1	-	70
2.3	54	14	5	28	-	-	-	101
2.4	62	19	13	-	2	-	-	96
2.5	33	12	5	1	2	-	2	55
2.6	43	7	6	-	4	-	-	60
2.7	116	25	12	-	1	-	2	156
2.8	69	26	13	-	-	-	1	109
2.9	60	28	10	-	2	-	1	101
All	712	235	194	91	48	21	7	1308

* includes four beech and one each of field maple, sycamore and yew

Established seedlings/bushes were recorded only in 1996, when they numbered 1308 (Table 3.5.9). Over half were hawthorn, whilst hazel, holly and blackthorn accounted for most the remainder. Most appeared to be recently established seedlings or suckers, but two hazels were from layered branches. Many were part-browsed by deer. They were particularly numerous in the first two sections of transect I, but thereafter became

increasingly scarce where lime was dominant or where dense bracken grew below a canopy of oak and birch. They were generally more numerous on transect II. The distribution matched that of the recruiting individuals/stems (Table 3.5.8), and with the areas where larger canopy gaps had developed (Figure 3.5.4). Hawthorn and hazel were both mainly restricted to sections one and two on transect I, but were widespread down transect II. Holly was more widely distributed. Blackthorn was closely linked to larger individuals on transect II, but the 43 seedlings in section two of transect I were not. Most hornbeam were close to the start of transect I, near to seed trees to the north.

3.5.2.3. Stem growth during 1986-96

The analysis of stem gbh/basal area growth included only the main species and combined stems from all parts of the transects. Two aspects were examined: (i) the relationship between the increment rate and initial size of stems; and (ii) the increment rate of stems in different crown position/size categories in 1998.

3.5.2.3.1. Main tree species

All the main tree species showed significant positive relationships between the gbh and basal area increment rates and the initial size of stems (i.e. larger stems generally increased more than smaller stems), albeit that all of the data sets had a lognormal distribution (Figures 3.5.5-6, Table 3.5.10). For all species the regressions based on changes in basal area rather than gbh accounted for more of the variation, and in both cases lime and ash had the most and oak the least variation included. The relative position of the regression lines indicated that: (i) many of the smaller ash stems grew rapidly, whilst most of the smaller lime and birch grew slowly; (ii) the largest lime tended to have grown faster than similar-sized birch and oak; and (iii) larger birch and oak grew at similar rates.

Figure 3.5.5: Relationship between the gbh increment and initial gbh of stems for the main tree species in the two permanent transects in Langley Wood over 1986-96. Symbols in blue = ash, green = lime, red = birch, black = oak. Parameters for the regression lines shown are given in Table 3.5.10. The regression line for ash excludes the two larger stems. Some symbols represent more than one stem

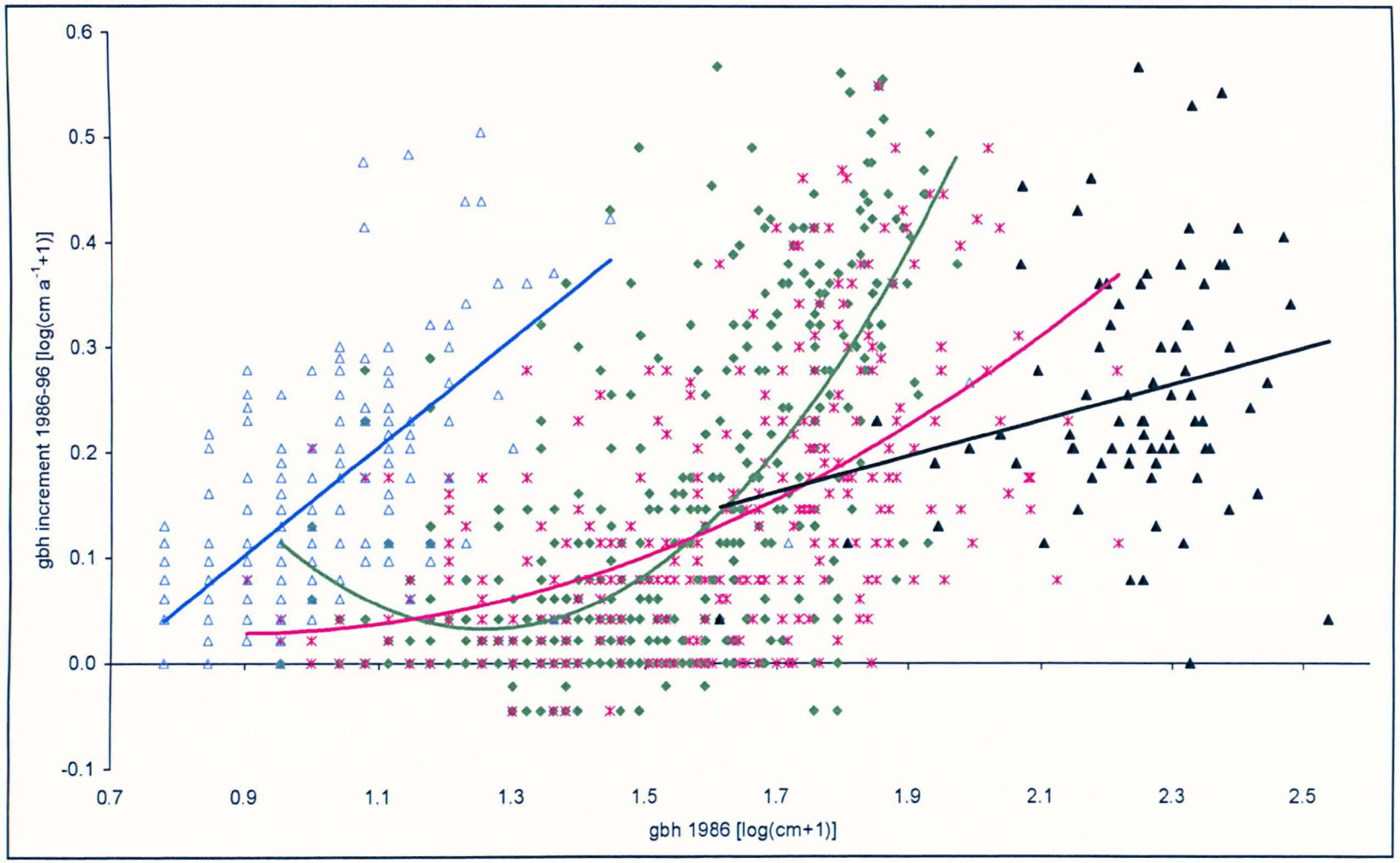


Figure 3.5.6: Relationship between the basal area increment and initial basal area of stems for the main tree species in the two permanent transects in Langley Wood over 1986-96. Symbols in blue = ash, green = lime, red = birch, black = oak. Parameters for the regression lines shown are given in Table 3.5.10. The regression line for ash excludes the two larger stems. Some symbols represent more than one stem

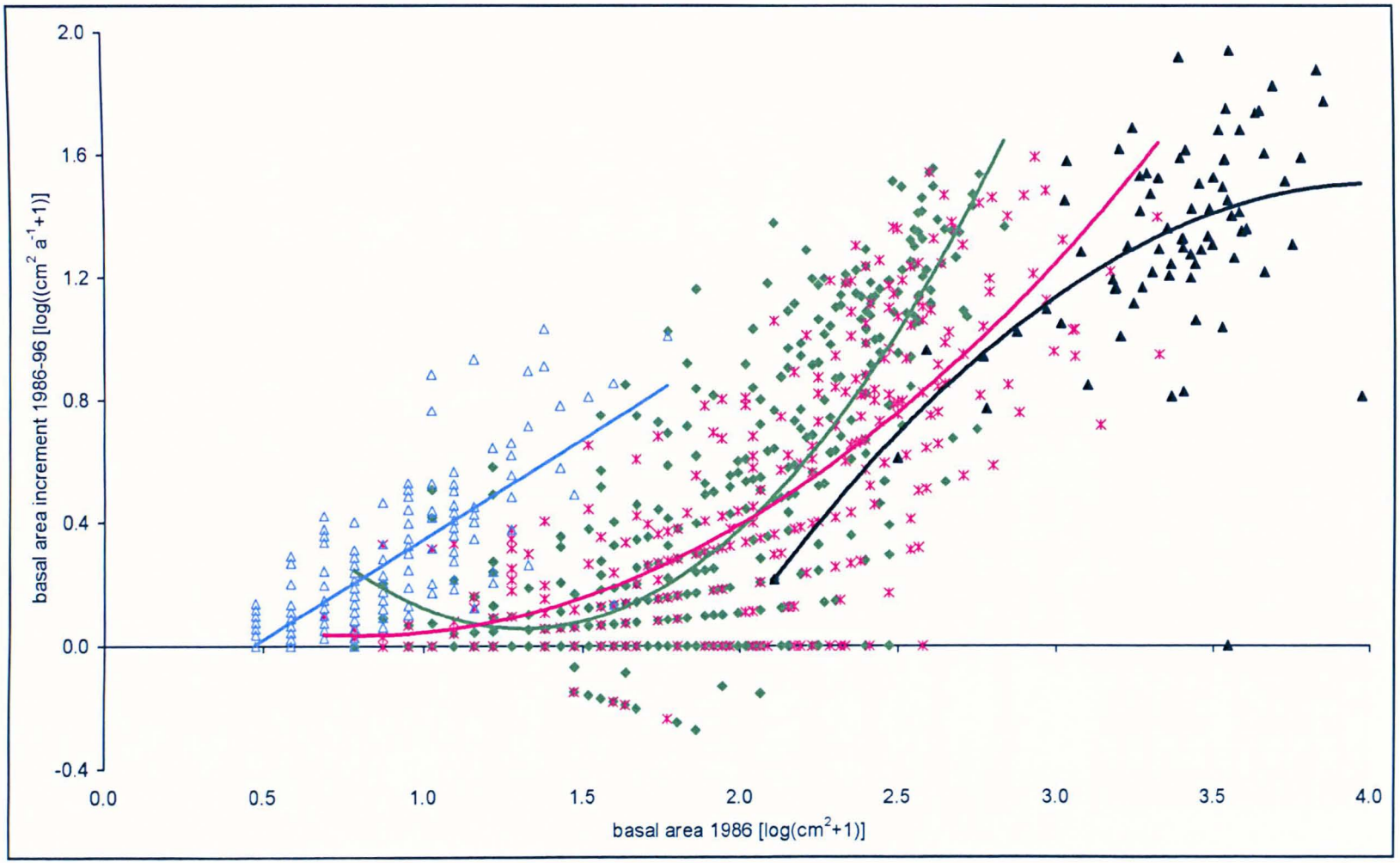


Table 3.5.10: Results of the stem increment analysis over 1986-96 for the main canopy/sub-canopy tree species in the two permanent transects in Langley Wood. The table shows the regressions comparing gbh increment (inc_{gbh}, cm a^{-1}) against initial gbh (ini_{gbh}, cm), and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2). Lognormal data were transformed before analysis. Figures 3.5.5-6 show the relationships as scatter plots

1. Gbh increment		**n**	**F**	**P**	**r^2%**
Lime	$\log(inc_{gbh+1}) = 0.8806.\log(ini_{gbh+1})^2 - 2.2165.\log(ini_{gbh+1}) + 1.4271$	446	201.3	<0.001	47.6
Ash*	$\log(inc_{gbh+1}) = 0.5144.\log(ini_{gbh+1}) - 0.3606$	209	170.7	<0.001	45.2
Birch	$\log(inc_{gbh+1}) = 0.1929.\log(ini_{gbh+1})^2 - 0.1787.\log(ini_{gbh+1}) - 0.3401$	292	61.5	<0.001	29.9
Oak	$\log(inc_{gbh+1}) = 0.1705.\log(ini_{gbh+1}) - 0.1265$	79	4.0	<0.05	5.0
2. Basal area increment					
Lime	$\log(inc_{ba+1}) = 0.6827.\log(ini_{ba+1})^2 - 1.7801.\log(ini_{ba+1}) + 1.2297$	444	403.2	<0.001	64.6
Ash*	$\log(inc_{ba+1}) = 0.6515.\log(ini_{ba+1}) - 0.3056$	209	312.6	<0.001	60.2
Birch	$\log(inc_{ba+1}) = 0.2510.\log(ini_{ba+1})^2 - 0.4018.\log(ini_{ba+1}) + 0.1948$	292	191.5	<0.001	57.1
Oak	$\log(inc_{ba+1}) = -0.3497.\log(ini_{ba+1})^2 + 2.8180.\log(ini_{ba+1}) - 4.1701$	79	16.8	<0.001	30.7

* excludes the two largest girth ash stems

Relationship between crown position/size and stem increment were examined (Table 3.5.11). It was expected that these would be positively related given that stem size generally increased as crown size increased and up through the crown layers (see section 3.5.6). For lime there was a relatively clear progressive relationship: larger crowned stems and those in the upper strata generally had higher increment rates than smaller stems in lower layers (Table 3.5.11a). Ash also showed a similar progression (Table 3.5.11b). For birch, two groups were evident: faster growing trees with small to large crowns in the canopy against all other trees (Table 3.5.11c). Although the rank order of the categories for oak followed a predictable pattern, significant differences were detected only between some of the basal area increment rates (Table 3.5.11d).

3.5.2.3.2. Main shrub species

Both of the main shrub species had significant relationships between the increment and initial gbh/basal area of stems. However, the trends were slight and differences between the regression lines were slight (Figure 3.5.7, Table 3.5.12). It was still notable that a substantial number of smaller hazel stems grew faster, as did a few medium hawthorn stems. Increment rates for hazel and hawthorn were examined in various crown position/size categories (Table 3.5.13). For hazel: (i) large or medium crowned categories

Table 3.5.11: Comparison of the increment rates over 1986-96 for stems in various crown position/size categories in 1996 for the four main tree species in the two permanent transects in Langley Wood. The table shows: (i) the median rate and mean rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the mean ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Lime ($H_{gbh\ (df=8)}$ = 286.7, $H_{basal\ area\ (df=8)}$ = 312.6, both P<0.001)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Canopy with medium crown	15	1.80	415.9	=bcd; >efghi (Q≥4.39)***
(b) Canopy with small crown	67	1.25	376.5	=acd; >efghi (Q≥5.21)***
(c) Sub-canopy medium crown	16	0.90	319.7	=abdef; >ghi (Q≥4.64)***
(d) Canopy with very small crown	23	0.60	314.5	=abcef; >ghi (Q≥5.01)***
(e) Sub-canopy small crown	48	0.33	240.4	<ab; =cdf; >gh (Q≥4.12)*; >i (Q=5.44)***
(f) Understorey medium crown	48	0.30	253.0	<ab; =cde; >g (Q=3.87)**; >hi (Q≥4.55)***
(g) Sub-canopy very small crown	26	0.05	134.8	<abcdef; =hi
(h) Understorey small/very small crown	163	0.05	128.4	<abcdef; =gi
(i) Ground all crown sizes	31	0.05	121.5	<abcdef; =gh
2. Basal area increment rates				
(a) Canopy with medium crown	15	23.49	423.3	=bcd; >efghi (Q≥4.45)***
(b) Canopy with small crown	67	12.06	381.7	=acd; >efghi (Q≥5.21)***
(c) Sub-canopy medium crown	16	6.47	324.4	=abdef; >ghi (Q≥4.58)***
(d) Canopy with very small crown	23	4.27	327.2	=abcef; >ghi (Q≥5.17)***
(e) Sub-canopy small crown	48	1.93	258.1	<ab; =cdf; >g (Q=3.81)**; >hi (Q≥5.03)***
(f) Understorey medium crown	48	1.66	237.0	<ab; =cdeg; >hi (Q≥4.30)***
(g) Sub-canopy very small crown	26	0.24	141.5	<abcde; =ghi
(h) Understorey small/very small crown	163	0.14	123.5	<abcdef; =gi
(i) Ground all crown sizes	31	0.11	112.5	<abcde; =fgh

(b) Ash ($H_{gbh\ (df=4)}$ = 117.1, $H_{basal\ area\ (df=4)}$ = 127.7, both P<0.001)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Sub-canopy with small crown	11	1.30	195.3	=b; >cde (Q≥3.99)***
(b) Sub-canopy with very small crown	12	0.80	170.6	=ac; >de (Q≥5.95)***
(c) Understorey with small crown	118	0.40	120.6	<a; =b; >de (Q≥5.20)***
(d) Understorey with very small crown	54	0.15	48.9	<abc; =e
(e) Ground all crown sizes	11	0.10	23.1	<abc; =d
2. Basal area increment rates				
(a) Sub-canopy with small crown	11	5.07	197.9	=b; >cde (Q≥4.07)***
(b) Sub-canopy with very small crown	12	2.14	176.1	=a; >c (Q≥3.03)*; >de (Q≥6.25)***
(c) Understorey with small crown	118	0.72	121.4	<ab; >de (Q≥5.37)***
(d) Understorey with very small crown	54	0.17	45.9	<abc; =e
(e) Ground all crown sizes	11	0.09	20.6	<abc; =d

(c) Birch ($H_{gbh\ (df=9)}$ = 147.1, $H_{basal\ area\ (df=9)}$ = 191.8, both P<0.001)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Canopy with large/medium crown	24	0.90	237.3	=be; >cdgj (Q≥3.62)*; >fhi (Q≥5.43)***
(b) Canopy with small crown	74	0.70	215.1	=ae; >cdgj (Q≥3.31)*; >fhi (Q≥5.29)***
(c) Understorey large/medium crown	22	0.40	147.9	<ab; =defgij; >h (Q=3.40)*
(d) Canopy with very small crown	31	0.30	153.0	<ab; =cefgij; >h (Q=4.14)**
(e) Sub-canopy medium crown	5	0.20	138.9	<ab; =cdfghij
(f) Sub-canopy small crown	39	0.20	113.2	<ab; =cdeghij
(g) Sub-canopy very small crown	8	0.10	103.3	<ab; =cdefhij
(h) Understorey small crown	72	0.10	78.7	<abcd; =efgij
(i) Understorey very small crown	11	0.10	72.2	<ab; =cdefghj
(j) Ground all crown sizes	4	0.05	58.5	<ab; =cdefghi

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Table 3.5.11: continued

2. Basal area increment rates				
(a) Canopy with large/medium crown	24	13.91	258.7	=be; >cdefghi (Q≥4.42)***
(b) Canopy with small crown	74	6.94	221.9	=ae; >cg (Q≥3.67)*; >dfhi (Q≥4.29)***
(c) Canopy with very small crown	31	2.99	154.6	<ab; =defgij; >h (Q=4.79)***
(d) Understorey large/medium crown	22	1.35	134.6	<ab; =cefgijh
(e) Sub-canopy medium crown	5	1.31	138.5	<ab; =cdfghij
(f) Sub-canopy small crown	39	1.05	115.5	<ab; =cdeghij
(g) Sub-canopy very small crown	8	0.53	107.6	<ab; =cdefhij
(h) Understorey very small crown	11	0.23	60.2	<abc; =defgij
(i) Understorey small crown	72	0.22	68.5	<ab; =cdefghj
(j) Ground all crown sizes	4	0.07	37.6	<ab; =cdefghi

(d) Oak ($H_{gbh\ (df=4)} = 7.8$, $P = 0.10$; $H_{basal\ area\ (df=4)} = 20.7$, $P < 0.001$)

1. Gbh increment rates	**n**	**median**	**mean rank**	**pair-wise comparison of ranks**
(a) Canopy with very large crown	9	1.20	50.1	=bcde
(b) Canopy with large crown	28	0.75	42.2	=acde
(c) Canopy with medium crown	29	0.65	36.3	=abde
(d) Canopy with small crown	5	0.55	22.0	=abce
(e) Sub-canopy/understorey all crown sizes	5	0.55	26.5	=abcd
2. Basal area increment rates				
(a) Canopy with very large crown	9	47.0	56.8	=b; >cde (Q≥2.81)*
(b) Canopy with large crown	28	25.0	46.0	=acde
(c) Canopy with medium crown	29	17.9	33.1	<a; =bde
(d) Canopy with small crown	5	10.2	16.9	<a; =bce
(e) Sub-canopy/understorey all crown sizes	5	7.8	17.0	<a; =bcd

Table 3.5.12: Results of the stem increment analysis for the main shrub species in the two permanent transects in Langley Wood over 1986-96. The table shows the regressions comparing gbh increment (inc_{gbh}, cm a^{-1}) against initial gbh (ini_{gbh}, cm), and basal increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2). Lognormal data were transformed before analysis. Figure 3.5.7 shows the relationships as scatter plots

1. Gbh increment		**n**	**F**	**P**	**r^2 %**
Hazel	$inc_{gbh} = -0.0096.ini_{gbh} + 0.4954$	767	12.1	<0.001	1.6
Hawthorn	$inc_{gbh} = -0.0034.ini_{gbh} + 0.3238$	74	3.4	0.07	4.6
2. Basal area increment					
Hazel	$\log(inc_{gbh+1}) = 0.0964.\log(ini_{gbh+1}) + 0.1383$	767	26.0	<0.001	3.3
Hawthorn	$\log(inc_{gbh+1}) = 0.1097.\log(ini_{gbh+1}) + 0.0728$	74	5.8	0.02	7.4

generally had higher rates than those with smaller crowns; and (ii) comparable crown sizes in the understorey mostly had higher rates than in the ground layer. For hawthorn, there were no significant differences between the gbh increment rates, but basal area rates tended to be higher for medium than smaller crowned stems.

Figure 3.5.7: Relationships between (left) the gbh increment and initial gbh of stems and (right) the basal area increment and initial basal area of stems, for hazel (blue symbols) and hawthorn (red symbols) in the two permanent transects in Langley Wood over 1986-96. Parameters for the regression lines shown are given in Table 3.5.12. Some symbols represent more than one stem

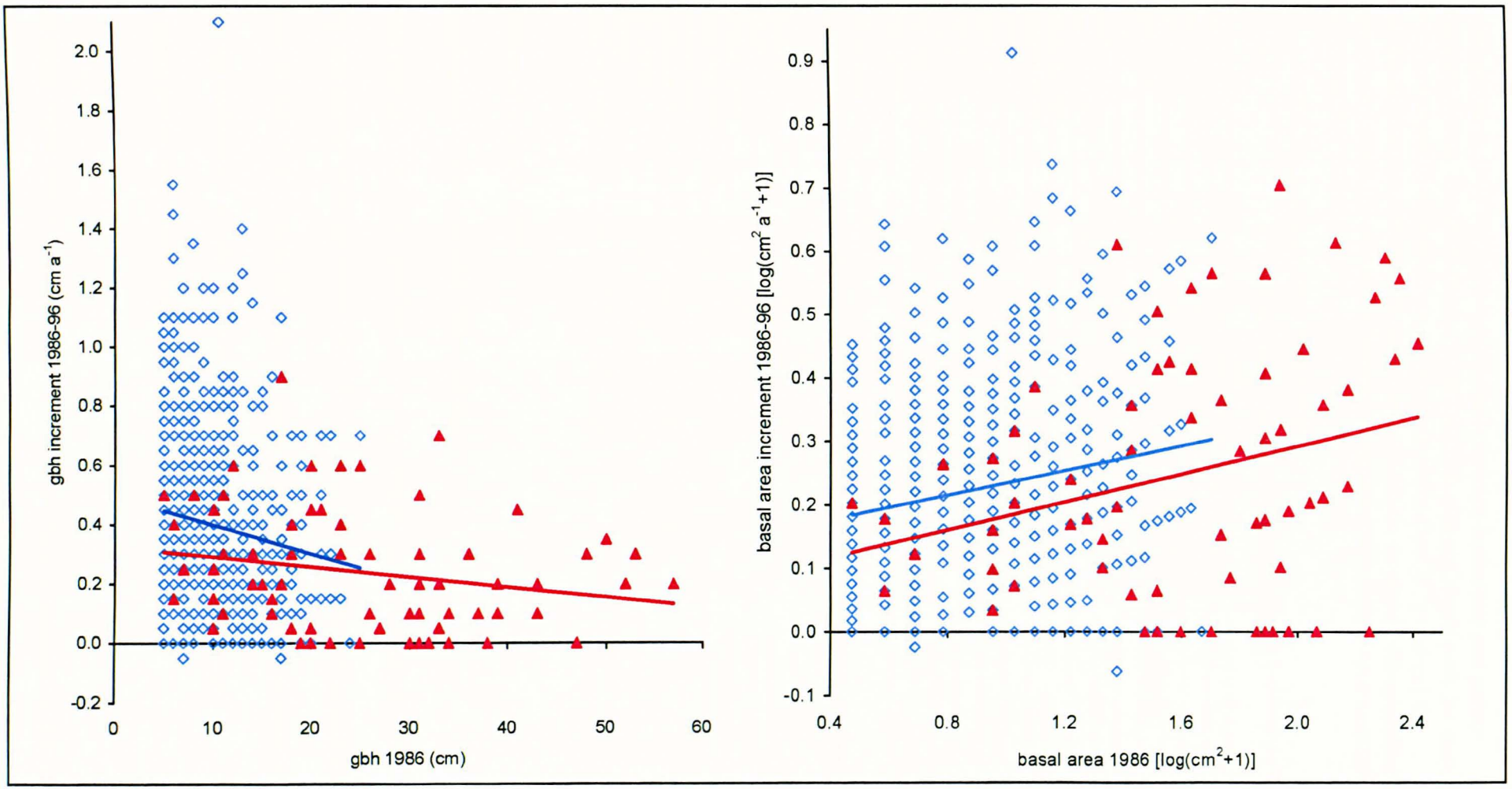


Table 3.5.13: Comparison of the increment rates over 1986-96for stems in various crown position/size categories in 1996 for the two main shrub species in the two permanent transects in Langley Wood. The table shows: (i) the median rate and mean rank for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the differences between the mean ranks based on an overall Kruskal-Wallis analysis of variance by ranks (H) test and subsequent nonparametric Tukey-type multiple comparison (Q) tests (*** = P<0.001, ** = P<0.01, * = P<0.05)

(a) Hazel ($H_{gbh\ (df=6)}$ = 129.7, $H_{basal\ area\ (df=6)}$ = 205.7, both P<0.001)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Ground large crown	15	0.70	488.5	=bcd; >efg (Q≥4.38)***
(b) Understorey medium crown	95	0.65	503.7	=a; >cdefg (Q≥4.73)***
(c) Understorey small crown	443	0.40	353.0	<b; =ad; >efg (Q≥4.40)***
(d) Ground medium crown	41	0.40	325.3	<b; =ace; >f (Q=3.31)*; >g (Q=3.60)**
(e) Ground small crown	66	0.20	235.9	<abc; =dfg
(f) Ground very small crown	21	0.10	146.2	<abcd; =eg
(g) Understorey very small crown	20	0.10	127.0	<abcd; =efg
2. Basal area increment rates				
(a) Understorey medium crown	95	1.62	569.4	=a; >cdefg (Q≥7.01)***
(b) Ground large crown	15	1.15	473.5	=bcd; >efg (Q≥4.48)***
(c) Understorey small crown	443	0.57	346.9	<a; =bd; >efg (Q≥4.96)***
(d) Ground medium crown	41	0.45	304.2	<a; =bce; > fg (Q=3.37)**
(e) Ground small crown	66	0.22	214.3	<abc; =dfg
(f) Understorey very small crown	20	0.13	102.0	<abcd; =efg
(g) Ground very small crown	21	0.09	121.3	<abcd; =eg

(b) Hawthorn ($H_{gbh\ (df=3)}$ = 1.6, p = 0.66; $H_{basal\ area\ (df=3)}$ = 9.3, P = 0.025)

1. Gbh increment rates	n	median	mean rank	pair-wise comparison of ranks
(a) Ground medium crown	8	0.25	36.9	=bcd
(b) Ground small crown	5	0.20	38.5	=acd
(c) Understorey medium crown	21	0.20	37.5	=abd
(d) Understorey small/very small crown	34	0.18	31.5	=abc
2. Basal area increment rates				
(a) Understorey medium crown	21	1.17	45.1	=bc; > d (Q=2.90)*
(b) Ground medium crown	8	0.72	34.2	=bcd
(c) Ground small crown	5	0.48	26.3	=acd
(d) Understorey small/very small crown	34	0.47	29.2	=abd

3.5.2.4. Condition of stems in 1996

3.5.2.4.1. Stratification, crown size and crown die back

Most live stems were given a crown position, crown size and die back category in 1996 (Table 3.5.14). The canopy layer accounted for 12% of stems, though a third had medium or larger crowns. In the lower three layers, the sub-canopy contained the least number of stems, whereas the understorey accounted for the most. In the lower layers a high percentage of stems had small or very small crowns.

Many recorded birch stems were in the upper two layers. Here, they accounted for 46% of canopy and 33% of sub-canopy stems. Although almost 40% of all birch stems were in the

understorey, they were relatively scarce in this stratum. Stratification and die back of birch are detailed in Table 3.5.15. The larger crowned trees in the canopy accounted for most of the largest gbh trees and these had no major die back. Progressively down through the stratum and as crown size decreased within each layer, the gbh size-range/mode fell whilst the degree of die back increased. Thus, the smallest gbh stems within each layer tended to have the smallest crowns and the most die back. Most canopy birch were erect and some appeared to be quite vigorous, whereas only about half in the sub-canopy were erect and very few were vigorous. Most die back appeared to be due to competition for growing space in the overstorey and shading in the lower stratum. However, a few wind-damaged trees had also suffered substantial crown loss and several were tipped over and recorded in the understorey or ground layers.

Table 3.5.14: Crown position and crown size for all recorded live stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. The table shows (upper part) the number of stems in each category and (lower part) the percentage of stems in each column with different crown sizes. Some stems were not recorded

	Canopy	Sub-canopy	Understorey	Ground	Not recorded
Birch	152	62	144	7	1
Lime	99	89	218	36	6
Oak	74	4	1	-	3
Ash	3	24	187	14	2
Hazel	-	-	1093	456	141
Hawthorn	-	1	87	45	7
Other species	3	10	31	9	-
All species	331	190	1761	567	160
Crown size					
% very large	3	-	<1	-	-
% large	9	-	1	2	-
% medium	21	14	13	15	-
% small	48	61	72	49	-
% very small	19	25	14	33	-

Lime occupied all of the crown layers. It had a similar number of canopy/sub-canopy stems as birch, but almost 60% of lime stems were in the lowest two layers. Comparing the relative frequency of stems, lime was less frequent in the canopy than birch and more frequent in the lower three layers (152 of 365 birch stems v 99 of 442 lime stems in

Table 3.5.15: Relationship between stem size, crown position and die back for all live birch stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. The table shows: (i) the number of stems in each gbh size-classes with a particular crown position; (ii) the number of stems with moderate [(m)] or severe/very severe die back [(s)]; and (iii) the number of larger stems that were fallen alive on ground [(F)] or were snapped/tipped and hung-up [(S)]. The last three rows show the percentage of stems in each column with different degrees of crown die back

Crown position:	Canopy				Sub-canopy			Understorey				Ground			
Crown size: Gbh size-class (cm)	Large	Medium	Small	Very small	Medium	Small	Very small	Large	Medium	Small	Very small	Large	Medium	Small	Very small
3-9.9	-	-	-	-	-	-		-	-	3 (2m)	2 (1s)	-	-	1 (1m)	1 (1s)
10-19.9	-	-	-	-	-	-		-	3	46 (15m,4s)	8 (6s)	-	-	2 (1m)	-
20-29.9	-	-	-	-	-	4	4 (1m,1s)	-	12 (1m)	44 (11m)	3 (3s)	-	-	-	-
30-39.9	-	-	1 (1s)	2	2	21 (3m)	4 (2s)	-	6	12 (3m,1s)	-	-	1 (1mF)	-	1 (1sF)
40-49.9	-	-	3 (1m)	14	2 (1m)	17 (2m)	-	-	2	1 (1s)	-	-	-	-	-
50-59.9	-	-	14 (1m)	13 (1m,1s)	-	4 (1sS)	1	-	-	-	-	-	-	-	-
60-69.9	-	1	30	5	-	-	-	1 (1s)	1 (1sS)	-	-	1 (1mF)	-	-	-
70-79.9	-	2	19 (1mS)	1 (1m)	-	1 (1S)	1	-	-	-	-	-	-	-	-
80-89.9	-	4	13 (1m)	-	-	-	-	-	-	-	-	-	-	-	-
90-99.9	-	3	8 (1mS)	1 (1sS)	-	1 (1m)	-	-	-	-	-	-	-	-	-
100-109.9	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-
110-119.9	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-
120-129.9	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-
130-139.9	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
140-149.9	-	-	-	1 (1sS)	-	-	-	-	-	-	-	-	-	-	-
150-159.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
160-169.9	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
170-179.9	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
All sizes	1	24	90	37	4	48	10	1	24	106	13	1	1	3	2
Die back															
% healthy/part	100	100	93	86	75	85	60	-	92	65	23	-	-	33	-
% moderate	-	-	6	5	25	13	10	-	4	29	-	100	100	67	50
% severe/very severe	-	-	1	9	-	2	30	100	4	6	77	-	-	-	50

Table 3.5.16: Relationship between stem size, crown position and die back for all live lime stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. Details as in Table 3.5.15

Crown position:	Canopy			Sub-canopy			Understorey				Ground		
Crown size: Gbh size-class (cm)	Medium	Small	Very small	Medium	Small	Very small	Very large/large	Medium	Small	Very small	Medium	Small	Very small
3-9.9	-	-	-	-	-		-	-	-	-	-	-	2
10-19.9	-	-	-	-	-	2 (1m)	-	-	31 (5m)	12 (6m,4s)	-	13 (4m)	3 (1s,1sF,1sS)
20-29.9	-	-	-	-	4 (1m)	7 (2m,1s)	-	16	70 (18m,3s)	17 (8m,9s)	3	6 (1m,2s)	1 (1F)
30-39.9	-	-	-	-	14 (2m)	10 (4m,2s)	-	16	29 (5m,3s)	6 (1m,5s)	3 (2m)	1 (1m)	4 (3sF,1sS)
40-49.9	-	-	6 (1m)	3	21 (1m)	6	-	7	4 (4m)	1 (1sS)	-	-	-
50-59.9	-	12	8 (1m)	6	7	-	1	4	-	-	-	-	-
60-69.9	-	20	5	3	2	-	2	-	-	1 (1sS)	-	-	-
70-79.9	-	14	3	3	1	-	-	-	-	-	-	-	-
80-89.9	7	9	1	-	-	-	-	1 (1m)	-	-	-	-	-
90-99.9	3	6	-	-	-	-	-	-	-	-	-	-	-
100-149.9	5	-	-	-	-	-	-	-	-	-	-	-	-
All sizes	15	61	23	15	49	25	3	44	134	37	6	20	10
Die back													
% healthy/part	100	100	91	100	92	60	100	98	72	5	67	60	30
% moderate	-	-	9	-	8	28	-	2	24	41	33	30	-
% severe/very severe	-	-	-	-	-	12	-	-	4	54	-	10	70

canopy; $\chi^2_{(df=1)} = 34.6$, $P<0.001$). Stratification and die back of lime are detailed in Table 3.5.16. The general trends were similar to birch, except that die back was scarce amongst canopy stems and none in the canopy or sub-canopy were wind-snapped. Most canopy/ sub-canopy stems were erect, but whilst many in the canopy appeared vigorous, few did in the sub-canopy. Stems in the understorey/ground layers included many that were arched over, leaning or growing laterally.

Oak was mainly recorded in the canopy and accounted for 22% of trees here. Most larger gbh oak had medium or larger crowns in the canopy with little die back (Table 3.5.17). Smaller trees tended to have smaller crowns with more die back, and the very smallest were mainly in the lowest strata. Much of the die back was due to exclusion from adjacent oak and lime crowns and many long-overtopped trunk boughs were dead or declining. However, one canopy tree had extensive crown deterioration and bough loss leaving a sizeable gap, and several trees had a few branches/boughs missing due to wind breakage.

Table 3.5.17: Relationship between stem size, crown position and die back for all live oak stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. Details as in Table 3.5.15

Crown position:	Canopy				Sub-canopy		Under-storey
Crown size: Gbh size-class (cm)	Very large	Large	Medium	Small	Medium	Small	Medium
40-59.9	-	-	-	-	-	1	-
60-99.9	-	-	-	1	-	2 (1m)	1
100-139.9	-	-	4 (1m)	2	1	-	-
140-179.9	-	4 (1m)	14 (2m,1s)	1 (1m)	-	-	-
180-219.9	2	12	11 (3m)	2 (1m,1s)	-	-	-
220-259.9	1	13 (1m)	-	-	-	-	-
260-299.9	3	1	-	-	-	-	-
300-339.9	2	-	-	-	-	-	-
340-379.9	1	-	-	-	-	-	-
All sizes	9	30	29	6	1	3	1
Die back							
% healthy/part	100	93	100	50	100	67	100
% moderate	-	7	-	33	-	33	-
% severe/very severe	-	-	-	17	-	-	-

Most ash had a small gbh and were in the understorey with only small crowns (Table 3.5.18). Only a few stems were in the canopy. These included the three largest gbh trees.

The canopy and sub-canopy ash were growing erectly and appeared healthy, even if they were small-crowned. Those in the lower strata were a mixture of erect, arched, leaning and lateral stems. 12% in the understorey and 86% in the ground layer had significant die back due to exclusion, most of which were within the smallest size-class. Two stems in the canopy and one in the sub-canopy were located well down transect II, having pushed up through the oak-dominated canopy. On transect I, two stems had grown into the sub-canopy and another 20 were in the understorey. Most of the remainder were located in or near the birch-ash stand at the start of transect II. These included a single canopy and 19 sub-canopy trees, most of which were growing up strongly below the broken canopy.

Table 3.5.18: Relationship between stem size, crown position and die back for all live ash stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. Details as in Table 3.5.15

Crown position:	Canopy		Sub-canopy		Understorey		Ground	
Crown size:	Medium	Very small	Small	Very small	Small	Very small	Small	Very small
Gbh size-class (cm)								
3-9.9	-	-	-	-	22 (2m)	51 (7m,2s)	2	11 (3m,8s)
10-19.9	-	-	-	6	96 (7m)	8 (1m)	1 (1m)	-
20-29.9	-	-	5	5	9 (1m)	-	-	-
30-39.9	-	-	7	1	1	-	-	-
40-49.9	-	1	-	-	-	-		-
50-59.9	-	1	-	-	-	-	-	-
100-109.9	1	-	-	-	-	-	-	-
All sizes	1	2	12	12	128	59	3	11
Die back								
% healthy/part	100	100	100	100	92	83	67	-
% moderate	-	-	-	-	8	14	33	27
% severe/very severe	-	-	-	-	-	3	-	73

Hazel had most stems in and accounted for almost two-thirds of those recorded in the understorey. However, it still accounted for 80% of stems in the ground layer, partly because many hazel stems were growing laterally. Few stems were adjudged as having large crowns and most were classed as small or very small. The larger gbh stems were mostly in the understorey with little die back, whereas the smallest included many of the smaller crowned stems in the understorey, most of the stems in the ground layer, and most of the stems with significant die back (Table 3.5.19). Most die back was due to exclusion, but some stems had been broken or bent over by fallen canopy branches. About half the

hazel stems in the understorey were classed as erect, and about three-quarters of these appeared vigorous. Most others were arched, leaning or lateral, and only 26% of these appeared vigorous. In the ground layer only about a quarter were erect. In both layers, proportionally less stems were classified as erect or vigorous as crown size increased.

Table 3.5.19: Relationship between stem size, crown position and die back for all live hazel stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. Details as in Table 3.5.15

Crown position:	Understorey			Ground			
Crown size:	Medium	Small	Very small	Large	Medium	Small	Very small
Gbh size-class (cm)							
3-9.9	-	277 (7m,1s)	123 (5m,1s)	-	25	176 (50m,3s)	132 (44m,25s)
10-14.9	10	389 (43m,1s)	7 (3m,2s)	8	34 (12m)	38 (15m,6s)	12 (3m,7s,2sS)
15-19.9	50	153 (22m,1s)	3 (2s,1sS)	7	10 (5m)	10 (8m,1s)	2 (2s)
20-24.9	46 (2m)	17 (3m,1mS,1s)	-	1	-	1 (1m,1sS)	-
25-29.9	16	2 (1mS,1s)	-	-	-	-	-
30-34.9	2	-	-	-	-	-	-
All sizes	124	838	133	16	69	225	146
Die back							
% healthy/part	98	90	89	100	75	62	43
% moderate	2	9	6	-	25	33	32
% severe/very severe	-	1	5	-	-	5	25

Hawthorn stems were mainly in the understorey or ground layers. About two-thirds were growing more or less erectly. Several established stems developed vigorous trunk shoots in response to canopy gaps. Stratification and die back of hawthorn are detailed in Table 3.5.20. The general trends were similar to hazel, though a couple of larger stems were in the ground layer, having fallen or been struck by a toppled oak. The relative frequency of hawthorn and hazel stems was similar in the understorey and ground layers, but hawthorn stems with large or medium crowns were more frequent (39 of 133 stems v 209 of 1551 stems; $\chi^2_{(df=1)} = 24.5$, $P<0.001$), and hawthorn stems with moderate or worse die back were also more frequent (41 of 133 v 283 of 1551 stems; $\chi^2_{(df=1)} = 12.5$, $P<0.001$).

In addition, the canopy contained one alder, beech and sweet chestnut, and whilst the sub-canopy contained a few beech, sycamore, yew and sweet chestnut. The most numerous additional species in lower two layers were beech, field maple and blackthorn.

Table 3.5.20: Relationship between stem size, crown position and die back for all live hawthorn stems ≥3cm gbh in the two permanent transects in Langley Wood in 1996. Details as in Table 3.5.15

Crown position:	Sub-canopy	Understorey			Ground		
Crown size:	Medium	Medium	Small	Very small	Medium	Small	Very small
Gbh size-class (cm)							
3-9.9	-	-	5	3	-	14 (1m)	11
10-19.9	-	3	26 (7m)	-	3 (3m)	5 (2m,1s)	2 (1s,1sF)
20-29.9	-	6	11 (7m,1s)	1 (1s)	7 (3m,1sS)	1 (1m)	-
30-39.9	-	8 (1mS)	11 (3m,1s)	-	-	-	-
40-49.9	-	5 (1m)	1 (1m)	2 (2sS)	1 (1sF)	1 (1sF)	-
50-59.9	1	4	-	-	-	-	-
60-69.9	-	1	-			-	-
All sizes	1	27	54	6	11	21	13
Die back							
% healthy/part	100	93	63	50	27	71	92
% moderate	-	7	33	-	55	19	-
% severe/very severe	-	-	4	50	18	10	8

3.5.2.4.2. Stem debarking by deer

A minority of stems in 1996 appeared to have been debarked by deer (Table 3.5.21), though it was not always clear which debarked stems had been stripped by squirrels or damaged by falling branches, etc. Only 56 stems were affected. These were all <20cm gbh and were <10cm gbh. Hazel had the most stems debarked by deer, including three that had been killed. Two small ash had also been killed. In addition, a few birch, crab apple, hawthorn and lime were debarked.

Table 3.5.21: Deer-debarking damage on all stems recorded in the two permanent transects in Langley Wood in 1996

	Standing dead, killed by debarking	Alive, severe debarking	Alive, moderate debarking	Alive, limited debarking
Hazel	3	5	22	12
Ash	2	2	1	2
Crab apple	-	1	-	-
Lime	-	1	-	-
Birch	-	-	2	-
Hawthorn	-	-	-	3
Total	5	9	25	17

3.5.2.4.3. Stem debarking by grey squirrels

A small number of stems were debarked by grey squirrels in 1996. These included two of the three sycamore: the largest 46cm gbh had lost its leader at 2m up probably due to

squirrel stripping, and the 20.5cm gbh stem had some basal damage. Also, a single hazel appeared to have been part-debarked by squirrels, and possibly two birch. More important was the debarking of all 20 live beech stems plus three others that were dead or alive only at the base (Table 3.5.22). These included: five that had much bark removed and were dead, crown-dead or ring-barked; 11 with severe debarking; and 18 that were at least moderately, including all >40cm dbh. Several had early crown yellowing, and just five live beech remained with limited debarking. The two dead stems, which had been killed by debarking, were the only two larger beeches that died between 1986-96.

Table 3.5.22: Debarking damage by grey squirrels to beech stems recorded on the two permanent transects in Langley Wood in 1996. The table shows the gbh of stems in different damage categories. Stems were alive apart from one alive only at the base and two that had died dead

Damage category	Gbh (cm)
Very severe	45, 34^{dead}, 29^{dead}, 24, 22$^{alive\ base\ only}$
Severe	56, 50, 42, 39, 29, 26, 25, 24
Moderate	65, 44, 42, 35, 29
Limited	36, 26, 26, 16, 9

3.5.2.5. Dead wood during 1986-96

3.5.2.5.1. Changes in snags

Changes in the basal area and density of snags from 1986 to 1996 are shown in Table 3.5.23. Although the density of snags changed little from 1986 to 1996, the basal area rose by almost 60%. Eight species formed snags, but only birch, hazel, lime and oak contributed much to the total basal area or density of snags. At both dates, birch was the most important species, followed by hazel. The main changes amongst the species were: (i) the increases in the basal area of birch and oak; and (ii) the increase in the density (but not basal area) of hazel. At both recordings, most snags remained small and few attained more than 40cm gbh.

The turnover of snags between 1986 and 1996 was substantial (Table 3.5.24). Only 8%

Table 3.5.23: Change in the basal area, density and relative importance of snags in the two permanent transects in Langley Wood between 1986 and 1996. Includes all dead standing stems ≥5cm gbh. Relative importance = [% total basal area + % all snags]÷2

	Basal area (m^2 ha^{-1})		Density (n ha^{-1})		Relative importance (%)	
	1986	1996	1986	1996	1986	1996
Birch	0.20	0.37	41	39	31	33
Hazel	0.08	0.06	54	72	23	25
Lime	0.11	0.11	45	33	23	16
Oak	0.10	0.27	1	4	9	17
Hawthorn	0.04	0.04	10	10	7	5
Ash	0.01	<0.01	18	9	6	3
Blackthorn	<0.01	<0.01	1	1	<1	<1
Beech	-	0.01	-	3	-	1
Total	0.54	0.86	169	171	100	100

Table 3.5.24: Fate, throughput and recruitment of snags in the two permanent transects in Langley Wood between 1986 and 1996. The table shows the number of snags in each category, including all dead standing stems ≥5cm gbh; (a) includes live stems in 1986 that had died and collapsed by 1996; (b) includes live stems in 1986 that had died and which formed snags in 1996; and (c) includes stems <5cm gbh, <1.3m tall or not present in 1986 and which formed snags in 1996

	Snags in 1986	Fate of 1986 snags by 1996		Throughput 1986-96	Recruitment 1986-96	
		Still standing	Collapsed	(a)	(b)	(c)
Hazel	60	9	51	88	55	17
Lime	50	1	49	72	36	-
Birch	46	3	43	108	41	-
Ash	20	1	19	94	9	-
Hawthorn	11	-	11	16	10	1
Oak	1	1	-	4	3	-
Blackthorn	1	-	1	1	1	-
Beech	-	-	-	1	2	1
Willow	-	-	-	1	-	-
All species	189	15	174	385	157	19

from 1986 remained standing in 1996, and of the snags present in 1996 only 8% had stood for over ten years. Percentage survival was: (i) similar across most size-classes (except the single the large oak survived); and (ii) high for oak (100%), and amongst the other species only hazel achieved above 10% survival. Throughput (i.e. live stems in 1986 that had died and collapsed by 1996) numbered 385, leaving 157 (29%) that died but formed snags in 1996. The percentage that formed snags was: (i) highest for stems ≥20cm gbh (38%) and least for stems of 5-<10cm gbh (23%); and (ii) highest for hawthorn and hazel (38%),

lower for lime and birch (28-33%), and least for ash (9%) (including species with >25 snags). In addition, a small number of snags (mostly hazel) recruited from stems that had grown over the 5cm gbh recording threshold during 1986-96 and then died.

3.5.2.5.2. Fate of large logs, large collapsed snags, and large trees that died

Table 3.5.25: Fate of large logs, large snags that collapsed and large trees that died between 1986 and 1996 as recorded in the two permanent transects in Langley Wood. In addition the status in 1986 of the larger logs recorded in 1996 is shown. The values are the number in each category

	Fate of logs 1986-96[a]			Fate of large snags that collapsed during 1986-96[d]	Fate of large live stems that died during 1986-96[e]			Status in 1986 of large logs in 1996[b]	
	Large log in 1996[b]	Small log in 1996[c]	Gone/in small pieces in 1996	Did not form large log in 1996	Formed snag in 1996	Formed large log in 1996[b]	Did not form large log in 1996	From logs in 1986	From live trees in 1986[f]
Birch	5	1	5	3	11	13	5	4	29
Oak	6	-	-	-	3	4	-	7	25
Hawthorn	-	-	-	1	-	-	2	-	1
Lime	-	-	-	-	-	-	1	-	-
All species	11	1	5	4	14	17	8	11	55

[a] includes all large fallen dead stems recorded in 1986; [b] includes fallen dead stems ≥40cm girth at their mid-point and ≥1m in length in 1996; [c] includes fallen dead stems smaller than criteria for large logs; [d] includes standing dead stems ≥40cm gbh in 1986; [e] includes live trees ≥40cm gbh in 1986; [f] includes 21 oak boughs snapped out of live trees, which might have been dead standing beforehand

The fate of the larger fallen dead logs plotted on the 1986 charts was examined, along with the fate of snags ≥40cm gbh that collapsed and trees ≥40cm gbh that died during 1986-96 (Table 3.5.25). Of the 17 larger logs in 1986, five had decayed away/were in small pieces in 1996. Of the 12 survivors, only 11 were classed as large logs (i.e. ≥40cm girth at the largest end and ≥1m in length). All of the oak logs survived (including two fallen trunks and four snapped crown boughs), but only about half the birch did. None of the four larger snags that collapsed made large logs in 1996. Of the 39 larger live trees that died, 14 formed snags and 17 formed large logs in 1996, leaving eight that did neither. All the oak involved formed either snags or large logs, whereas only 24 of the 29 birch did, and none of the hawthorn or lime did.

It was also possible to identify the status in 1986 of 66 large fallen logs recorded in 1996 (Table 3.5.25). Most (55) were from live birch or oak trees, though 21 of the oak involved were boughs snapped out of live trees and could have been dead standing in 1986. The remaining 11 logs had been recorded as logs in 1986, including seven oak and five birch.

3.5.2.5.3. Dead wood levels, dimensions and condition in 1996

The abundance, dimensions and condition of snags and fallen dead logs/branches was assessed in detail in 1996 (Table 3.5.26). The combined volume and length of these was $22m^3\ ha^{-1}$ and $2405m\ ha^{-1}$ respectively, approximately 70% of which was lying on the ground. The individually measured large logs accounted for about half of the volume and a quarter of the length of all logs/branches, though these were sampled differently.

Most snags were <30cm gbh, <7m tall, had limited decay and/or much of their bark still present (Table 3.5.26). Much of the total volume was split between oak and birch, and birch, hazel and lime accounted for much of the total length and density. Most hazel snags were short or medium height with a small gbh, whilst most taller and large gbh snags were oak, birch or lime. Most logs/branches were also <30cm girth at the point of intersection, and many had limited decay and retained much of their bark (Table 3.5.26). Compared to snags, however, they were generally more decayed and had less bark: 15 out of 45 logs/branches were rotten or very rotten compared to only 18 out 199 snags ($\chi^2_{(df=1)} = 18.5$, $P<0.001$); and only 27 out of 45 logs/branches retained 50% or more bark compared to out 136 out of 148 snags ($\chi^2_{(df=1)} = 26.7$, $P<0.001$). Oak and birch accounted for 89-95% of the total volume and length of logs/branches. Only four logs measured 50cm girth or more at the point of intersection, including two oak and two birch. Similarly, most of the individually measured large logs were oak or birch, <60cm girth at the base, and 5m or more in length. Only oak logs/branches formed of heartwood appeared substantially resistant to long-term decay.

Table 3.5.26: Quantity and condition of dead wood, including snags and all fallen dead logs/branches as recorded in the two permanent transects in Langley Wood in 1996. Cells show the number of snags/logs in each category unless stated otherwise

(a) Snags – based on measurements of snags ≥5cm gbh

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Height			Gbh			Decay state			Remaining bark		
				0-2.5m	3-7m	>7m	5-<30cm	30-<60cm	60-142cm	Solid/part-rotten	Rotten/ very rotten	Not recorded	<50%	50-100%	Not recorded
Oak	3.8	44	3	-	-	4	-	-	4	4	-	-	1	3	-
Birch	2.4	241	39	9	26	15	33	13	4	44	4	2	1	44	5
Lime	0.6	135	29	10	20	7	33	4	-	31	4	2	10	25	2
Hazel	0.2	208	82	64	38	2	104	-	-	80	10	14	-	49	55
Hawthorn	0.2	33	10	5	8	-	10	3	-	12	-	1	-	10	3
Ash	<0.1	52	8	1	9	-	10	-	-	9	-	1	-	4	6
Beech	<0.1	8	3	2	2	-	4	-	-	1	-	3	-	1	3
Blackthorn	<0.1	2	1	-	1	-	1	-	-	1	-	-	-	-	1
All species	7.1	722	175	91	104	28	195	20	8	181	18	23	12	136	75

(b) All fallen logs/branches – based on line transect survey of fallen dead stems ≥15cm girth at point of intersection

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Girth at point of intersection			Decay state		Remaining bark	
			15-<30cm	30-<50cm	50-67cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Oak	7.7	972	19	5	2	19	7	16	10
Birch	6.6	524	10	2	2	8	6	1	13
Lime	0.5	112	3	-	-	3	-	1	2
Hazel	0.2	37	1	-	-	-	1	-	1
Hawthorn	0.2	37	1	-	-	-	1	-	1
All species	15.1	1683	34	7	4	30	15	18	27

(c) Large individually mapped logs – based on measurements of fallen logs ≥40cm girth at the largest end and ≥1m in length

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Girth at base			Length		
				40-<60cm	60-<80cm	80-97cm	1-4.5m	5-9.5m	10-28m
Oak	4.4	198	25	22	10	2	8	11	13
Birch	3.3	205	25	1	-	-	6	16	10
Hawthorn	<0.1	4	1	30	13	11	-	1	-
All species	7.7	407	51	53	23	13	14	28	23

3.6. Stand change and natural disturbance at Clairinsh

3.6.1. Introduction

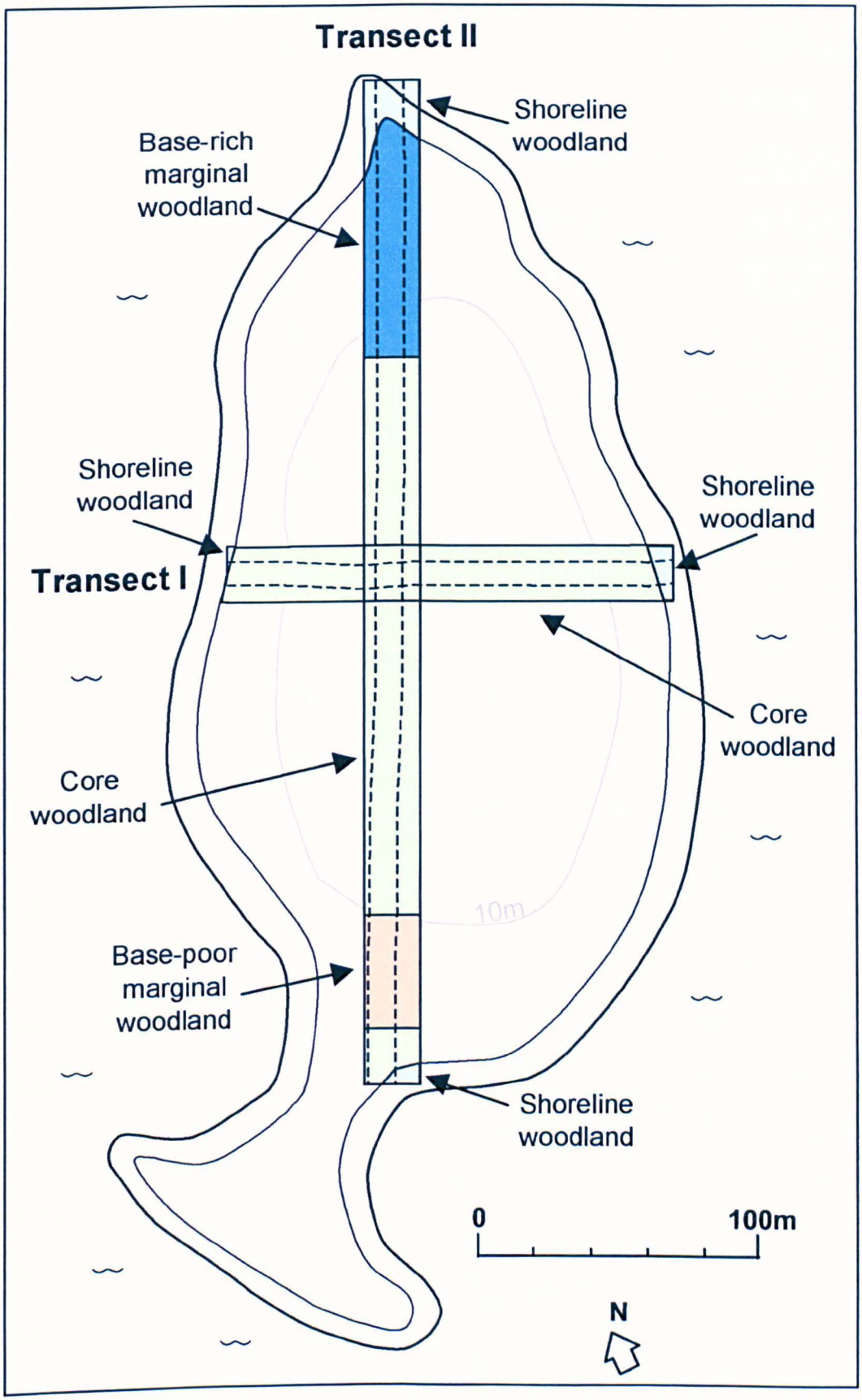
3.6.1.1. Site details

Clairinsh is an uninhabited island in the southern part of Loch Lomond, central Scotland (see Figure 2.1, Table 2.1). Tittensor (1969, 1970), Placido (1986), and Backmeroff & Peterken (1989) give details of the site and its history, management, and flora and fauna. It is one of the ancient, semi-natural oakwoods within the Loch Lomond National Nature Reserve, and is managed by Scottish Natural Heritage under a long-term lease.

The island covers 6ha, is oval in shape and has the longest axis heading towards NNE (Figure 3.6.1). Much of the central part forms a plateau at about 5m above the level of the loch or 14m above sea level. The soils here are free-draining, moderately acidic, brown earths. The shoreline is periodically inundated and mostly occurs as a narrow, platform shelf, made of sandy alluvium and boulders and with a 1-2m tall bank where it adjoins the main part of the island. However, at the northern tip of the island and some other places there is a shingle beach. In between there is some marginal, low-lying, poorly-drained ground. At the northern end of the island this carries moderately base-rich stagnogley soils, whereas at the southern end the associated soils are base-poor stagnogleys.

The higher ground is covered mainly pedunculate/sessile oak and downy birch growing over an understorey of rowan, holly and hazel (see Appendix for scientific names of species). The ground vegetation is dominated either by bluebell or greater wood rush, with other common species including bracken, bramble, honeysuckle and ivy. This vegetation corresponds mostly to community W11 of the National Vegetation Classification (Rodwell 1991) and stand type 6B of Peterken (1993). The low-lying, base-rich marginal woodland at the northern end of the island (Figure 3.6.1) has much ash, oak and downy birch, growing over blackthorn and common hawthorn and other minor species. Bluebell and

Figure 3.6.1: Map of Clairinsh Island showing the main features and location of the two permanent transects studied. The dashed lines mark the 10m-wide transects laid out in 1961 by Ken Wallace and subsequently encompassed within the 20m-wide transects laid out in 1986 by Christa Backmeroff. Four types of woodland crossed by the transects are shown



bracken dominate the ground vegetation. The low-lying, base-poor woodland at the southern end has mostly alder, downy birch and oak growing over rowan, holly and hazel. Bluebell dominates the ground vegetation. On the shoreline shelf the ground flora is more mixed and contains plants characteristic of damp conditions. This woodland includes much grey willow, ash, alder, pedunculate oak and downy birch, and other minor species. On the shingle beach areas, grey willow, alder and birch predominate close to the loch, whilst mixed ash woodland occurs on the shelf directly above up to the high-water strand-line. Thus, the low-lying marginal woodland represents communities W6/7 and the shoreline woodland community W1/2 in the National Vegetation Classification (Rodwell 1991).

Traditionally the wood was managed as coppice-with-standards, with oak promoted as the main tree. Several species were enhanced/introduced by plantin, including pedunculate oak, ash, beech, hornbeam, larch, Scot's pine and sycamore. The last major felling took place in 1913, when most of the underwood was cut and a scatter of oak standards and singled oak stools retained. The wood left to naturally regenerate and has since been kept under a minimum-intervention regime. It was part-damage by a severe windstorm in January 1968, and some non-native trees were cut out: (i) during 1970-71, when some beech, larch and rhododendron were felled; and (ii) in 1998 when a western red cedar was felled. In addition, boating visitors have made and collected firewood for a few campfires.

3.6.1.2. Recording

Details of the aims of recording and methodologies used are given in Section 2.4 and Table 2.3. Two permanently marked and more or less straight transects were used for recording (see Figure 3.6.1). These were positioned along the main axes of the island and include areas of all the main woodland types. They extended for 174m and 362m. Details of the transect recording are given in Table 3.6.1. The first recording took place during 1960-62, when Ken Wallace accurately mapped the trees and shrubs and other features

Table 3.6.1: Details of the records made in the permanent study transects at Clairinsh

Date of recording	Features recorded
1960-62	• All individuals with the largest live stem ≥1 inch quarter girth (10cm gbh), including their location, species and status – many individuals below this girth threshold were also recorded, but no minimum threshold was stated. • Gbh of the largest live stem ≥1 inch quarter girth (10cm gbh), including only the largest stem on coppice stools and holly groves (a few additional stems were included), taken as a quarter girth to nearest inch (2.5cm). • Top height of all live stems ≥1 inch quarter girth (10cm gbh) and, on larger trees, the height to first main branch, measured to the nearest foot (0.3m). • Extent of areas covered by dense low-groves of holly. • Supplementary notes on the presence of climbers, epicormic growth and the number of coppice stems. • Various salient features. • Age of twenty oaks scattered along the transects and covering a wide range of sizes – this was done by taking two trunk cores, counting the growth rings, and estimating an allowance for any missing rings (most cores did not touch the exact centre, so the average number of rings per inch was determined and then related to the girth proportionally – since the early annual increments were probably wider on average than later increments, the estimated ages were likely to be greater than the true ages).
June 1986	• All individuals ≥1.3m height, giving their location, species and status. • Gbh of all live and dead stems ≥5cm gbh and many below, measured to nearest cm; • Position of various larger fallen dead logs (criteria not specified), often with a gbh measurement for the largest end and indication of the species. • Various salient features.
April 1998	• All individuals ≥1.3m height, all established seedlings and dense patches of low-holly, giving their location and status. • Gbh of all live and dead stems ≥5cm gbh, to nearest half cm. • Condition of live stems, including allocation of a crown position (this proved somewhat problematic in the low-growing, open-canopied parts of stands) and descriptive notes (brief notes for smaller live stems, fuller descriptions for canopy trees), and cause of demise for stems that had been lost, including details of all large windblown trees. • Height and description of decay state for all snags ≥10cm gbh. • Fallen dead wood abundance and condition – this was done using two line transects positioned along the mid-line of the two transects and measuring the girth or diameter (to nearest cm) of all fallen dead stems ≥15cm girth where they crossed the lines – notes were made on the origin and condition of each piece. • Extent of canopy gaps and notes on their origin and understorey infilling. • Various salient features.

within both transects, producing a set of scale transect charts, three profile diagrams of the stands (each covering three sections, 60m length), and a report. The transects were made 11 yards (10m) wide. Each was subdivided into sections of one chain (20m) length, with the sections being numbered from the western (transect I) or northern (transect II) end. Collectively, they covered 0.5ha or 9% of the island area. Most fieldwork appeared to have been done in summer 1961. The transects were recording again in June 1986 by Christa

Backmeroff, who managed to relocate the original transects (with some difficulty), including some of the original marker posts. A decision was made to widen the transects to 20m, encompassing all the ground recorded in 1961 transects within them (for some reason the first 12m at the start of transect I was not included). The widened transects covered 1ha or 18% of the island area. Most records made were drawn onto a set of A4 scale charts, each covering a 30m long transect section. The last recording took place during April 1998. It included all the ground recorded in 1986.

3.6.1.3. Analysis

The approach to the analysis and statistics used are discussed and detailed in Section 2.5. Firstly, the analysis focused on the general changes in stand composition and structure since the last major felling in 1913 and up to 1961, based on an assessment of the stand characteristics when the transects were first recorded. A more detailed analysis of stand changes during 1961-1986 and 1986-98 was made by comparing the features recorded at these dates and by an assessment of the additional features recorded in 1998.

Changes were examined: (i) from 1961-1986-1998 using the 0.5025ha from the 10m wide transects initially recorded by Wallace in 1961; and (ii) from 1986-1998 using the 1.005ha from the 20m wide transects initially recorded by Backmeroff in 1986. The transects were subdivided into five stand types, as distinguished by their topography, soil status and stand composition (Section 3.6.1.1, Figure 3.6.1, Table 3.6.2): (i) most of the sections were classed as 'core woodland', as they occurred on the higher, central part of the island with free-draining, brown earth soils; (ii) the low-lying parts of the northern and southern ends of transect II with gley soils were classed as 'base-rich marginal woodland' with abundant ash or as 'base-poor marginal woodland' with abundant alder; and (iii) the small areas at the transect ends that extended onto the shoreline shingle beach or platform shelf were classed as 'shoreline shingle woodland' or 'shoreline shelf woodland'. The marginal and

Table 3.6.2: Area of the five woodland stand types included within the permanent transects on Clairinsh

Stand	Area within Wallace transects		Area within Backmeroff transects	
	ha	%	ha	%
Core woodland	0.3550	71	0.7020	70
Base-rich marginal woodland	0.0890	18	0.1675	17
Base-poor marginal woodland	0.0400	8	0.0800	8
Shoreline shingle woodland	0.0100	2	0.0305	3
Shoreline shelf woodland	0.0085	2	0.0205	2
All	0.5025	100	1.0005	100

shoreline woodland were examined in less detail as they provided only small samples.

The data set provided information on 4190 stems/individuals/seedlings/logs. A small number of mistakes and apparent errors were corrected for and various assumptions were made. The main problems were with stem relocation and gbh measurements on complex, multi-stemmed and forked individuals, particularly because: (i) the small-scale of the 1961 charts made them difficult to read and several dense holly thickets were simply mapped as 'groves' with only the largest stem measured; (ii) most additional trunk shoots and side forks that arose below 1.3m height appeared to have been omitted in 1961 and 1986; and (iii) some complex stools were not sketched clearly or at all.

Various standard measures were calculated, with annual rates of change from 1961 to June 1986 and to April 1998 being based on 25 and 11.5 growing seasons respectively. Separate species of birch, oak and willow were aggregated. The basal area within the 10m-wide Wallace transects was calculated using only individual with stems ≥10cm gbh and using only the largest stem on each, whilst in the Backmeroff transects all stems ≥5cm gbh could be used. Although it was not certain that in 1961 all individuals <10cm gbh had been recorded and the lower threshold for individuals was 5cm gbh, for the analysis it was assumed that this was the case or nearly so. This allowed the number of 'small individuals'

in 1961 (i.e. with the largest stem <10cm gbh) to be compared to the number in 1986 and 1998 with the largest stem at 5-<10cm gbh.

3.6.2. Results

3.6.2.1. Change in the core woodland

3.6.2.1.1. Stand development before 1961

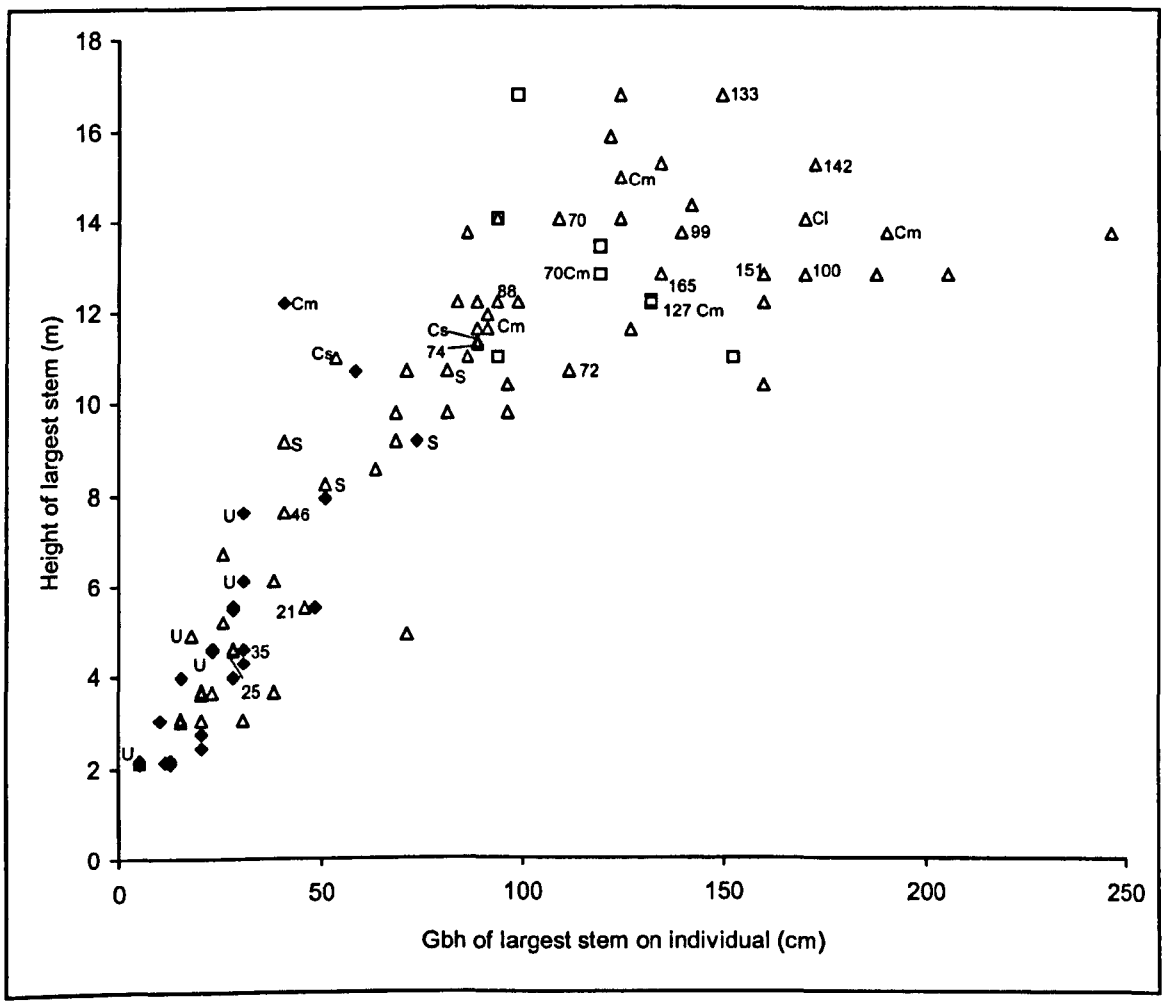
This woodland type covered much of the island (Figure 3.6.1). It was crossed by parts of both transects and some sections were included on two of the stand profile diagrams. By 1961 it had developed into dense, closed, high forest with twelve tree and shrub species recorded within the transects (Table 3.6.3). It mainly comprised an overstorey of oak with some birch and a few alder, ash, beech, larch and Scots pine, and an understorey of smaller birch, holly, rowan and hazel, plus a few small broom and yew. The basal area was almost $24m^2\ ha^{-1}$. The gbh size-distribution of the largest stems on each individual revealed a scatter of larger trees (which must have been retained in 1913) and numerous smaller stems (indicative of abundant regeneration). It was difficult to decide exactly which individuals had been retained from 1913, but those ≥70cm gbh gave a density of 158 trees ha^{-1}.

Oak dominated the basal area in 1961 and accounted for most medium-large individuals (Table 3.6.3), which had presumably been retained in 1913. These included some retained standards, some coppice stools that been singled, and perhaps a few uncut coppice stools (Figure 3.6.2). Most were >10m tall, >75cm gbh and in the upper canopy. The ages of those that were cored ranged from 70 to 165 years, indicating that a progression of trees had been promoted during the past-coppicing system. Transect II passed close to one of the few very large oaks on the island: this was measured at 356cm gbh and at 279 years old, and had a wide, spreading crown that had developed in open conditions during the 18-20th centuries when the island was under regular coppice management.

Table 3.6.3: Basal area, density and size-class distribution for live individuals/stems in the permanent transects in the core woodland on Clairinsh in 1961. The basal area was based on the largest stem on each individual and only included stems ≥10cm gbh. On small individuals the largest stem was <10cm gbh (it was not certain that all of these were recorded)

		Basal area (m^2 ha^{-1})	Large individuals (n ha^{-1})	Small individuals (n ha^{-1})	Gbh size-class (cm) (n stems)									
					<10	10-<30	30-<50	50-<70	70-<90	90-<110	110-<130	130-<150	150-<250	All sizes
Major species	Oak	19.1	259	11	4	23	13	7	12	11	8	7	11	96
	Birch	2.2	248	34	12	59	21	5	1	1	-	1	-	100
	Holly	0.6	90	237	84	24	4	4	-	-	-	-	-	116
	Rowan	0.5	144	132	47	41	10	-	-	-	-	-	-	98
	Hazel	0.3	70	37	13	23	2	-	-	-	-	-	-	38
Minor species	Larch	0.5	3	-	-	-	-	-	-	-	-	1	-	1
	Ash	0.2	3	-	-	-	-	-	-	1	-	-	-	1
	Pine	0.2	3	-	-	-	-	-	1	-	-	-	-	1
	Alder	<0.1	6	-	-	-	2	-	-	-	-	-	-	2
	Beech	<0.1	3	-	-	-	1	-	-	-	-	-	-	1
	Broom	-	-	17	6	-	-	-	-	-	-	-	-	6
	Yew	-	-	9	3	-	-	-	-	-	-	-	-	3
	All species	23.7	828	476	169	170	53	16	11	13	8	9	11	463

Figure 3.6.2: Relationship between gbh and top height for the largest stem on oak individuals in the permanent transects in the core woodland on Clairinsh in 1961. ◆ = coppice; □ = promoted from coppice; △ = maiden; C = canopy; l = large crown; m = medium crown; s = small crown; S = sub-canopy; U = understorey (as determined from profile diagrams); numbers = age of stems in years (as determined from cores). Rank correlation coefficient, $r_s = 0.902$, $P<0.001$

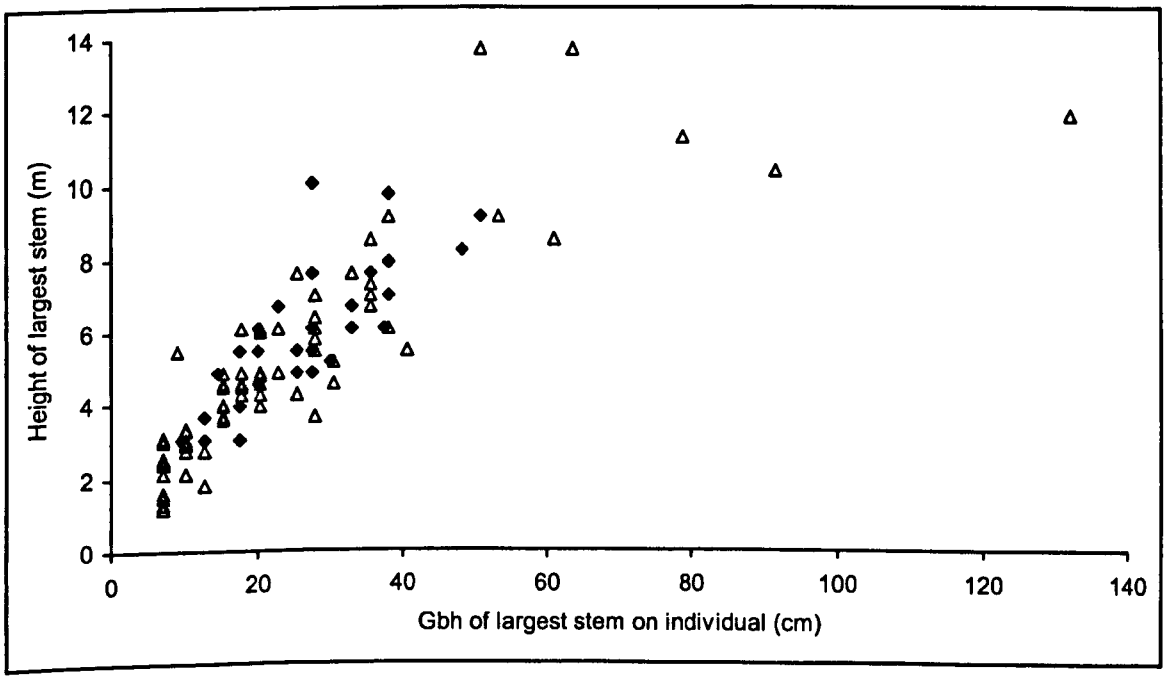


Post-1913 oak regeneration included a similar number of scattered of coppice and seedling recruits. The coppice individuals and at least some maidens could have established immediately. However, two maidens were aged at 21-25 years, suggesting that some took several years to reach 1.3m height (albeit that the method of ageing was not precise and suppressed trees could have produced indistinct growth rings). By 1961 virtually all of the recruits had failed to grow into the upper canopy (most were in the understorey and <6m tall), and most of the coppice stools had thinned to one or a few stems. Evidently, the retained trees retained in 1913 had generally shaded and suppressed them, partly because

some of the maidens appeared to have been slow in establishing and presumably because the weakest coppice individuals would have been selected for felling in 1913.

Birch was the second most abundant species in 1961, accounting for almost 10% of the basal area and 21% of individuals (Table 3.6.3). The few recorded large gbh, canopy birch were probably trees retained in 1913 (Figure 3.6.3). However, most individuals were small-medium gbh and indicated that post-1913 regeneration of birch had been abundant, and no doubt enhanced by the retained birch seed trees. Most recruits were maidens, but a scatter of multi-stemmed individuals had developed, many of which were probably of coppice origin. By 1961 most were overtopped, suppressed and growing in the understorey. Only a very few had made it into the upper canopy, including several coppice individuals where one or two stems had become dominant. Thus, despite substantial regeneration, the retained oak and other trees from 1913 had largely prevented birch recruits from developing into canopy trees.

Figure 3.6.3: Relationship between gbh and top height for the largest stem on birch individuals in the permanent transects in the core woodland on Clairinsh in 1961. ◆ = multi-stemmed, probably of coppice origin; △ = single-stemmed, probable maiden. Rank correlation coefficient, $r_s = 0.891$, $P<0.001$



A moderately dense, shade-tolerant understorey of holly and rowan had developed widely by 1961. Most individuals were relatively small (Figures 3.6.4-5, Table 3.6.3) and appeared to have established recently. However, at least the largest holly seemed to have been left uncut in 1913. Many of the larger rowan were multi-stemmed, possible coppice individuals, which appeared to have grown vigorously after being cut in 1913. Some of the smaller holly individuals and those in the two groves (which were located a short distance above the shoreline stand, in areas well-lit by side-light) were from low-layers that had established around larger bushes. Other small holly individuals had established from seed some distance from parent trees and often around the base of mature oaks.

Hazel also formed a part of the understorey in 1961 (Figure 3.6.6), though it was less abundant than rowan or holly (Table 3.6.3). Hazel individuals were widely distributed, but many occurred in sections close to where the two transects crossed. The largest had presumably regrown after coppicing in 1913. Several of these had many stems and remained reasonably vigorous, but the two with largest gbh stems had few additional stems and were surrounded by standard oaks and appeared to be in decline. Smaller gbh individuals may have been advanced forms of the latter or alternatively they could have been recent recruits. On multi-stemmed hazels, some of the smallest stems might also have established recently.

Variation in the abundance of the main species within the transects was examined by comparing the basal area of large stems on large individuals and the density of individuals using data in 15 available entire transect sections (6-15 on transect II, 1-2 and 5-7 on transect I; each 202m^2 in area). Only one significant rank correlation was found, between the density of large oak and all rowan individuals ($r_s = 0.564$, $P<0.05$), indicating that rowan had tended to develop better under or around oak.

Figure 3.6.4: Relationship between gbh and top height for the largest stem on holly individuals in the permanent transects in the core woodland on Clairinsh in 1961. Only individuals with reliable height measurements are included. Stems recorded as <10cm gbh are shown as 5cm gbh. Rank correlation coefficient, $r_s = 0.903$, $P<0.001$

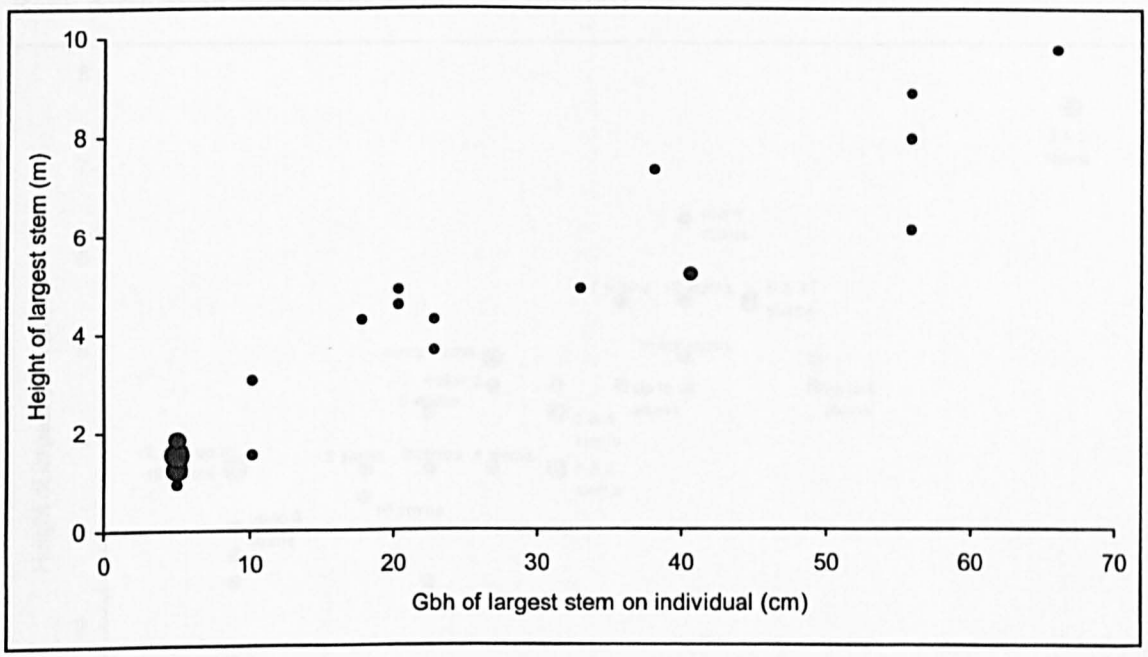


Figure 3.6.5: Relationship between gbh and top height for the largest stem on rowan individuals in the permanent transects in the core woodland on Clairinsh in 1961. Stems recorded as <10cm gbh are shown as 5cm gbh. The size of each point represents one to seven individuals. The total number of stems on multi-stemmed individuals is also shown. Rank correlation coefficient, $r_s = 0.818$, $P<0.001$

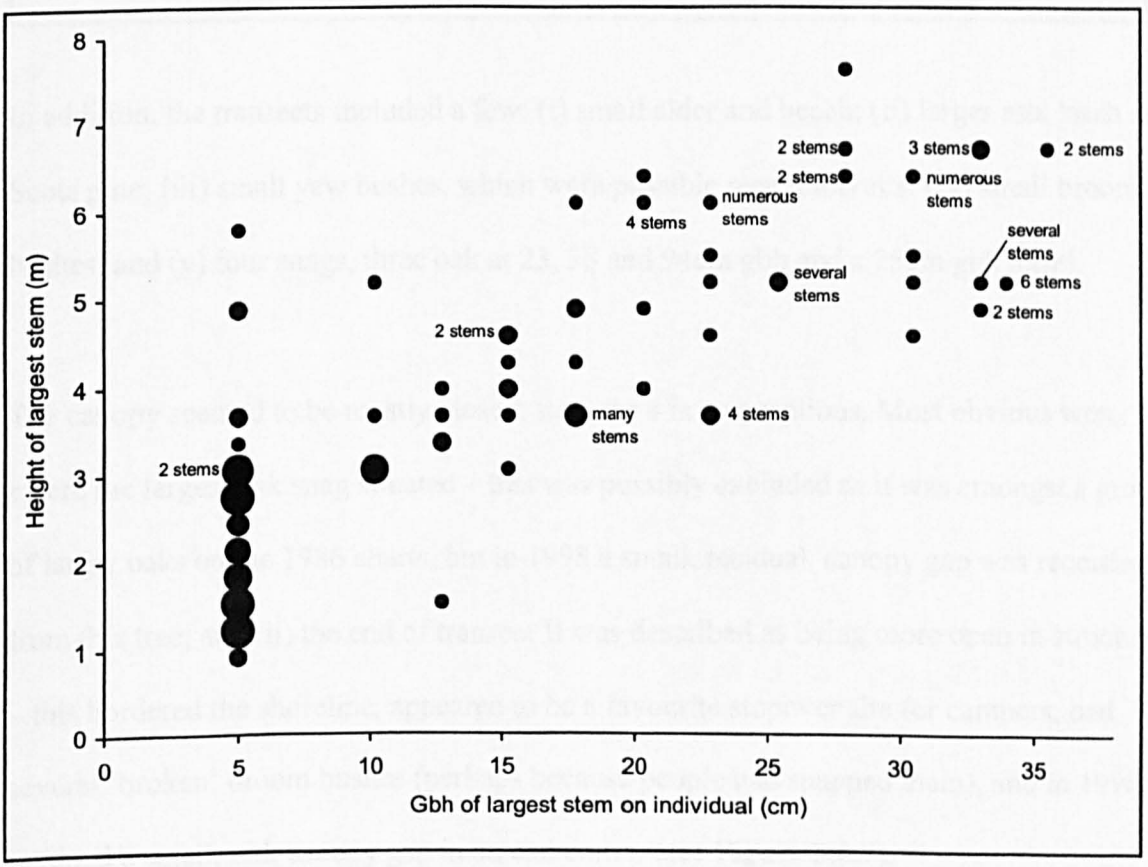
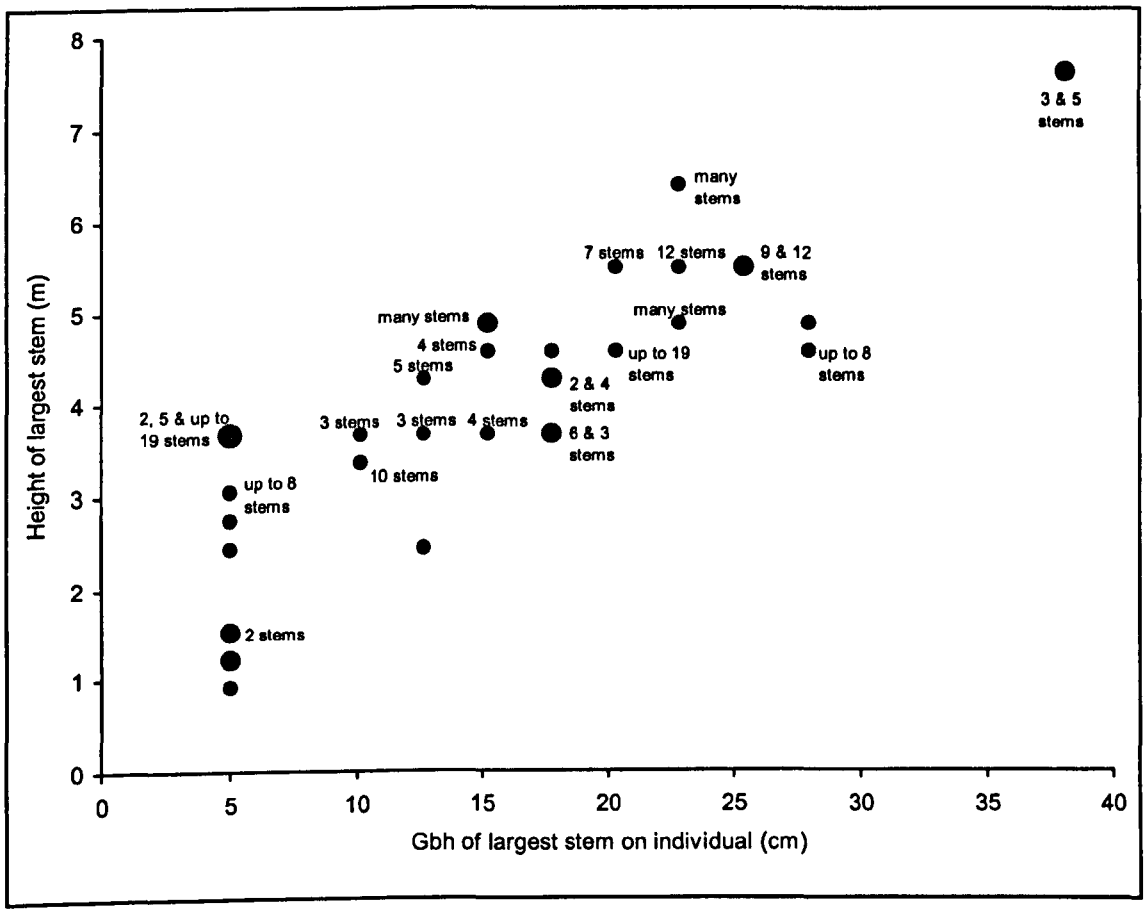


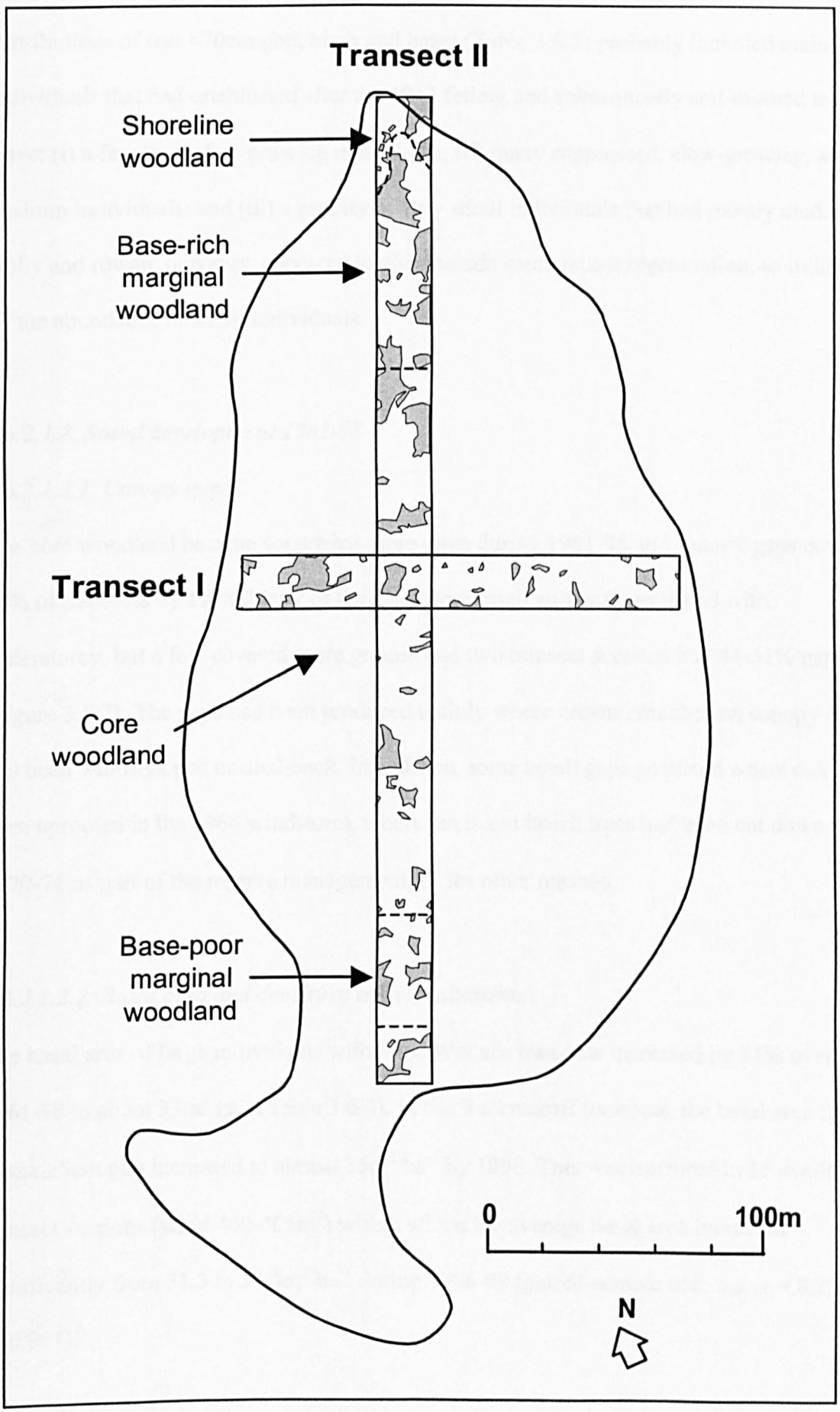
Figure 3.6.6: Relationship between gbh and top height for the largest stem on hazel individuals in the permanent transects in the core woodland on Clairinsh in 1961. Stems recorded as <10cm gbh are shown as 5cm gbh. The size of each point represents one to three individuals. The total number of stems on multi-stemmed individuals is also shown. Rank correlation coefficient, $r_s = 0.873$, $P<0.001$



In addition, the transects included a few: (i) small alder and beech; (ii) larger ash, larch and Scots pine; (iii) small yew bushes, which were possible recent recruits; (iv) small broom bushes; and (v) four snags, three oak at 23, 28 and 94cm gbh and a 25cm gbh hazel.

The canopy seemed to be mostly closed, save for a few exceptions. Most obvious were: (i) where the largest oak snag situated – this was possibly excluded as it was amongst a group of larger oaks on the 1986 charts, but in 1998 a small, residual, canopy gap was recorded from this tree; and (ii) the end of transect II was described as being more open in structure – this bordered the shoreline, appeared to be a favourite stopover site for campers, had several 'broken' broom bushes (perhaps because people had snapped them), and in 1998 retained a small, old, canopy gap in an end corner (see **Figure 3.6.7**).

Figure 3.6.7: Location of canopy gaps (shaded) along the permanent transects on Clairinsh Island in 1998



The lack of gaps combined with the size-distribution of live individuals to show that that competitive exclusion had been a major process during the preceding decades. The size-distributions of oak <70cm gbh, birch and hazel (Table 3.6.3) probably included mainly individuals that had established after the 1913 felling and subsequently self-thinned to leave: (i) a few large, fast-growing individuals; (ii) many suppressed, slow-growing, small-medium individuals; and (iii) a paucity of very small individuals that had mostly died. Holly and rowan, however, appeared to also include some recent regeneration, as indicated by the abundance of small individuals.

3.6.2.1.2. Stand development 1961-98

3.6.2.1.2.1. Canopy gaps

The core woodland became somewhat more open during 1961-98 and canopy gaps covered 16% of transects by 1998. Many of the gaps were small and/or under-filled with understorey, but a few covered more ground and two transect sections had 44-51% gaps (Figure 3.6.7). The gaps had been produced mainly where crown branches on canopy oak had been windsnapped or died-back. In addition, some small gaps persisted where oak had been uprooted in the 1968 windstorm, where larch and beech trees had been cut down in 1970-71 as part of the reserve management, or for other reasons.

3.6.2.1.2.2. Basal area and density of individuals/stems

The basal area of large individuals within the Wallace transects increased by 41% over 1961-98 to about 33m^2 ha^{-1} (Table 3.6.4). In the Backmeroff transects, the basal area for all stems ≥5cm gbh increased to almost 35m^2 ha^{-1} by 1998. This was mirrored in 15 available transect sections (sized 400-405m^2) within which the average basal area increased significantly from 31.3 to 34.3m^2 ha^{-1} during 1986-98 (paired-sample test: $t_{(df=14)} = 8.2$, $P<0.001$).

Table 3.6.4: Basal area, density and relative importance of live individuals/stems in the permanent transects in the core woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh; small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh; basal area on the Wallace transect was based on the largest stem on each individual and only included stems ≥10cm gbh; basal area on the Backmeroff transect included all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

		Basal area (m^2 ha^{-1})					Density large individuals (n ha^{-1})					Density small individuals (n ha^{-1})					Relative importance (%)				
		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect	
		1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998
Major species	Oak	19.1	24.5	26.7	24.3	26.0	259	211	197	201	185	11	17	6	14	6	51	49	48	46	45
	Birch	2.2	2.2	2.6	2.8	3.0	248	149	124	188	155	34	11	6	14	9	16	9	8	12	11
	Holly	0.6	1.6	2.4	2.4	3.3	90	347	383	295	325	237	256	194	254	219	14	24	26	24	26
	Rowan	0.5	1.0	1.3	1.5	1.8	144	242	259	219	221	132	73	45	63	40	12	13	14	13	13
	Hazel	0.3	<0.1	<0.1	0.1	0.1	70	28	37	23	30	37	39	37	67	70	5	3	3	4	4
Minor species	Larch	0.5	-	-	-	-	3	-	-	-	-	-	-	-	-	-	1	-	-	-	-
	Pine	0.2	0.5	0.6	0.2	0.3	3	3	3	1	1	-	-	-	-	-	<1	<1	1	<1	<1
	Ash	0.2	-	-	-	-	3	-	-	-	-	-	-	-	-	-	<1	-	-	-	-
	Beech	<0.1	<0.1	<0.1	<0.1	<0.1	3	3	3	3	3	-	-	-	-	3	<1	<1	<1	<1	<1
	Alder	<0.1	-	-	<0.1	<0.1	6	-	-	3	3	-	-	-	-	-	<1	-	-	<1	<1
	Yew	-	<0.1	<0.1	<0.1	0.2	-	9	9	11	13	9	-	6	3	4	<1	<1	<1	<1	<1
	Crab apple	-	-	-	<0.1	<0.1	-	-	-	1	1	-	-	-	-	-	-	-	-	<1	<1
	Hawthorn	-	-	-	<0.1	<0.1	-	-	-	1	1	-	-	-	1	-	-	-	-	<1	<1
	Broom	-	-	-	<0.1	-	-	-	-	-	-	17	3	-	1	7	<1	<1	-	<1	<1
	All species	23.7	29.8	33.4	31.5	34.9	828	992	1014	947	939	476	400	293	417	358	100	100	100	100	100

Amongst the main species, oak continued to dominate the basal area, increasing by 40% over 1961-98 and accounting for 80-82%/75-77% of the total basal area within the Wallace/Backmeroff transects (Table 3.6.4). Birch changed little in basal area, whereas rowan and holly both increased strongly, with respective increases of 2 to 4-5% and 3 to 7-10% of the total basal area within the Wallace/Backmeroff transects. In addition, hazel basal area decreased strongly during 1961-86.

The density of large individuals increased progressively in the Wallace transects over 1961-98, but changed little in the Backmeroff transects over 1986-98 (Table 3.6.4). In contrast, the density of small individuals fell. There were only slight changes in the density (1778 to 1793ha^{-1}) and size-distribution of stems ≥5cm gbh in the Backmeroff transects during 1986-98.

Amongst the main species, individuals of oak and birch decreased, which was the major cause of their decline in relative importance. Both also had higher declines during 1961-86 and higher percentage losses for small individuals. In contrast, large individuals of rowan and holly both increased substantially and especially during 1961-86 (though changes in holly relied on a reliable reconstruction of the 1961 population and this may have underestimated). However, only small individuals of holly remained numerous. Overall, holly increased from 25 to 42-44% of all individuals, whereas rowan remained around 20-23%. Hazel individuals decreased during 1961-86, mostly due to the reduction in large individuals, but thereafter numbers steadied.

Amongst the nine other minor species recorded: (i) yew increased notably in basal area and density of both large and small individuals; (ii) the single large Scots pine survived and increased substantially in gbh/basal area; (ii) the single large larch and beech present in 1961 were felled as part of a programme of reserve management to remove exotic trees,

but by two beech saplings left near the original tree grew vigorously and by 1998 two beech saplings and a seedling at 1.2m height had established elsewhere; (iii) the two alder in the Wallace transects became overtopped and died by 1986, but two other alder survived in the understorey in the Backmeroff transects; (iv) the single large ash was toppled during the 1968 windstorm and died; (v) most of the small broom bushes from 1961 were dead in 1986, but by 1998 several replacement bushes had established nearby and others just below 1.3m height were present; and (vi) a few hawthorn and crab apple recorded within the Backmeroff transects survived.

3.6.2.1.2.3. Survival, mortality and recruitment patterns

The fate and recruitment of individuals/stems is shown in Tables 3.6.5-7. Of 294 large and 169 small individuals recorded in 1961, 193 large and 144 small individuals remained alive in 1998. Thus, the overall mortality rates (m) for large and small individuals were 1.15 and 0.44% a^{-1} respectively. The mortality rate for large individuals fell from 1.49% a^{-1} over 1961-86 (on the Wallace transects) to 0.67-0.78% a^{-1} over 1986-98 (within the Wallace/Backmeroff transects). The rate for small individuals increased from 0.61% a^{-1} over 1961-86 to 1.97-2.27% a^{-1} over 1986-98. Rates were highest for individuals of 10<40cm gbh with relatively few dying sized <10cm gbh or ≥40cm gbh in 1961. Of the individuals that died over 1961-86 and 1988-98 (within the Wallace/Backmeroff transects), 22-27% formed snags at the end, the percentage being greater for large (26-37%) than small (4-24%) individuals. Recruitment of individuals went from 29ha^{-1} over 1961-86 (on the Wallace transects) to 13-15ha^{-1} over 1986-98 (on the Wallace/Backmeroff transects).

3.6.2.1.2.4. Survival, mortality, recruitment and condition of the main species in 1998

Large oak individuals suffered low mortality (m = 0.6-0.9% a^{-1} over the two periods in the Wallace/Backmeroff transects) and no trees over 100cm gbh in 1961 died. However, mortality rates for stems <40cm gbh were high, and many of the remaining small,

Table 3.6.5: Mortality, reduction and recruitment of large live individuals in the core woodland in the permanent transects in the core woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh. The table shows the number of stems in each category

	Wallace transect													Backmeroff transect				
	1961	1961-86					1986	1986-98						1986	1986-98			
	Alive	Died	Reduced to <10cm gbh	Died or reduced & formed snag at end	Recruited & <10cm gbh in 1961	Recruited & not recorded in 1961	Alive	Died	Reduced to <10cm gbh	Died or reduced & formed snag at end	Recruited & ≥10cm gbh in 1961 & <10cm gbh in 1986	Recruited & <10cm gbh in 1961 & 1986	Recruited & <10cm gbh in 1986	Alive	Died	Reduced to <10cm gbh	Died or reduced & formed snag at end	Recruited & <10cm gbh in 1986
Oak	92	19	-	7	1	1	74	5	-	3	-	-	-	141	11	-	7	-
Birch	88	38	2	8	5	-	53	9	-	3	-	-	-	132	23	-	9	-
Rowan	51	8	1	1	28	16	86	1	2	-	-	7	2	154	9	2	-	12
Holly	32	1	1	1	78	15	123	3	5	3	-	3	18	207	5	5	5	31
Hazel	25	11	6	6	2	-	10	-	1	-	3	1	-	16	-	2	-	7
Alder	2	2	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Beech	1	1	-	1	-	1	1	-	-	-	-	-	-	2	-	-	-	-
Pine	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-
Ash	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Larch	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Yew	-	-	-	-	3	-	3	-	-	-	-	-	-	8	-	-	-	1
Crab apple	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Hawthorn	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
All species	294	82	10	24	117	33	351	18	8	9	3	11	20	665	48	9	21	51

Table 3.6.6: Mortality, survival, development and recruitment of small live individuals in the core woodland in the permanent transects in the core woodland on Clairinsh in 1961, 1986 and 1998. Small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh. The table shows the number of stems in each category

	Wallace transect															Backmeroff transect					
	1961	1961-86						1986	1986-98							1986	1986-98				
	Alive	Died	Reduced to <5cm gbh	Died or reduced & formed snag at end	Grown to ≥10cm gbh	Recruited & ≥10cm gbh in 1961	Recruited & not recorded in 1961	Alive	Died	Reduced to <5cm gbh	Died or reduced & formed snag at end	Grown to ≥10cm gbh	Recruited & ≥10cm gbh in 1986	Recruited & <5cm gbh in 1986	Recruited & not recorded in 1986	Alive	Died	Died or reduced & formed snag at end	Grown to ≥10cm gbh	Recruited & ≥10cm gbh in 1986	Recruited & not recorded in 1986
Holly	84	1	-	-	78	1	85	91	17	-	5	21	4	14	4	178	30	6	31	5	32
Rowan	47	4	-	-	28	1	10	26	3	-	-	9	2	-	-	44	9	-	12	2	3
Hazel	13	2	2	1	2	5	2	14	-	1	-	4	1	4	-	47	6	2	7	2	13
Birch	12	6	-	-	5	2	1	4	3	-	-	-	-	-	1	10	5	-	-	-	1
Broom	6	5	-	-	-	-	-	1	1	-	-	-	-	-	4	1	1	-	-	-	5
Oak	4	3	-	-	1	-	6	6	4	-	2	-	-	-	-	10	6	2	-	-	-
Yew	3	-	-	-	3	-	-	-	-	-	-	-	-	-	2	2	-	-	1	-	2
Hawthorn	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-
Beech	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
All species	169	21	2	1	117	9	104	142	28	1	7	34	7	18	11	293	58	10	51	9	58

Table 3.6.7: Mortality rates (m% a^{-1}) for individuals of different sizes in the Wallace permanent transects in the core woodland on Clairinsh between 1961 and 1998. Based on initial size of largest stem on each individual. Some size-classes were not represented (-) and in some classes all stems died

Gbh size-class (cm)	Oak	Birch	Holly	Rowan	Hazel	Alder, ash, beech, broom, larch	Pine, yew	All species
<10	3.73	2.37	0.31	0.13	0.46	4.79	none	0.46
10-<20	3.73	2.80	0.86	0.16	2.29	-	-	1.54
20-<40	2.54	2.00	0.23	none	1.23	all	-	1.39
40-<60	0.32	1.10	-	none	-	all	-	0.58
60-<80	0.50	1.10	-	-	-	-	-	0.69
80-<100	0.30	none	-	none	-	all	none	0.38
100-<120	none	-	-	-	-	-	-	none
120-<140	none	all	-	-	-	-	-	0.26
140-<160	none	-	-	-	-	all	-	0.79
160-<220	none	-	-	-	-	-	-	none
All sizes	0.90	2.16	0.52	0.12	1.25	6.36	none	0.86

post-1913 recruits died (Tables 3.6.5-7). In addition, only a few of the post-1913 recruits managed to maintain above average growth. Most mortality was linked to the exclusion of individuals <40cm gbh. Some of these were recorded as snags, whilst the remainder probably died standing, including some that appeared to have been snapped off as snags by people for firewood. In addition, two larger trees at 69-94cm gbh appeared to have been excluded by adjacent large canopy oaks. Three other large oak (41, 99, 125cm gbh) were lost: two died during 1961-86 after being uprooted in the 1968 windstorm, whilst the other was wind-snapped during 1986-98.

Another four uprooted oak were recorded within or across the transects in 1986. Combining all six uprooted trees, these ranged from 41-158cm gbh and fell approximately towards ENE-ESE. A map of all the large oak and birch on the island that were windblown in 1968 (Figure 2 in Backmeroff & Peterken 1989), showed the same pattern of fall and a concentration of windthrown trees along the western side of the island. Five of the six windblown oaks associated with the transects were already dead in 1986. However, the survivor remained alive through to 1998 and had developed a low vigorous crown from an

upper fork, but had no basal sprouts. The windthrown trees that died remained as solid trunks in 1998, though their crown branches were mostly gone and only one tree retained a covering of bark under a thick layer of moss. The associated root mounds and hollows were still visible, but some mounds had slumped and most were now covered by ground vegetation. Vigorous new regeneration of birch and rowan was present at only one mound site, but some tipped holly bushes had re-sprouted at another.

Notable wind damage was recorded on 32 surviving oak trees in 1998. Some had been damaged long ago, perhaps first in the 1968 windstorm, but others had been damaged later and some had lost limbs quite recently. The affected trees included: (i) 23 at 108.5-306cm gbh that had branches snapped out but remained in the canopy; (ii) eight at 16-81.5cm gbh that had been relegated to the sub-canopy or understorey, having been hit by other falling trees or large branches and left growing on a lean/laterally and/or with much of the crown broken off; and (iii) a 141cm gbh tree, which was the uprooted tree from 1968 that remained alive on the ground. All that had lost large amounts of crown grew little over 1986-98. Collectively they represented 21% of the surviving trees and 33% of the oak ≥120cm gbh. A few had or were replacing lost crown growth, mainly from vigorous sprouts that were growing from immediately below where the stem had been broken. Several other trees showed signs of growth release, with obvious signs of vigorous crown expansion, sprout growth and/or top-growth, associated with canopy gaps.

Recruitment of new oak individuals was very limited and occurred only during 1961-86 (Tables 3.6.6-7). These individuals may well have been present in 1961 but were too small to have been included in the recording.

Mortality of large birch individuals was relatively high (m = 1.6-2.2% a^{-1} over the two periods in the Wallace/Backmeroff transects), and the population of small birch suffered

even more (m = 2.5-5.8% a^{-1}). Overall, it had the highest mortality rate of all the main species (Tables 3.6.5-7). Most losses were <45cm gbh and <10m height in 1961 and appeared to have been excluded. However, a few of the post-1913 recruits managed to remaining relatively fast-growing and some made it into the canopy. The two larger birch deaths were connected with storm-damage (a 132cm gbh tree was uprooted in the 1968 windstorm; and a 64 cm gbh tree was recorded with its top snapped off in 1986) and one small tree died after being crushed by a large, uprooted ash.

Another three uprooted birch were recorded in or across the Backmeroff transects in 1986. Three fell towards ENE-E (as did other trees uprooted in 1968), but the other had fallen towards SSE. Only one tree was alive on the ground in 1986, but this had died by 1998. By this time two of the trunks were rapidly rotting away, all the associated root mounds had slumped, and no new regeneration had developed in the vicinity. Ten surviving birch in 1998 had been storm-damaged, including a group of larger trees that had been tilted on to each other and seven understorey individuals that had been struck by windblown trees or canopy debris. In contrast, several birch in the canopy and understorey had been released with obvious signs of vigorous crown expansion associated with gaps in the canopy.

Recruitment of birch over 1961-98 was minimal (Tables 3.6.6-7) and restricted to a very few saplings that developed below gaps created by the 1968 windstorm. Of the few smaller girth birch that grew well and reached the canopy, one was released after the windthrow of an adjacent canopy oak in 1968 and was still ascending vigorously below the gap in 1998.

Large rowan individuals suffered low mortality (m<0.7% a^{-1} over the two periods in the Wallace/Backmeroff transects), and recruitment, which mostly comprised slow-growing, small seedlings, far exceeded the small number of losses (Tables 3.6.5-7). However, by 1998 there were signs that recruitment was beginning to wane: the overall density of small

individuals actually decreased, the mortality rate for these increased (0.4% a^{-1} in 1961-86 to 1.1-2.0% a^{-1} in 1986-98), and individuals <1.3m height in 1998 amounted to only five established seedlings and two areas where pinned branch ends were layering. Rowan losses were concentrated in the smaller size-classes, with most being <20cm gbh. Although this implicated exclusion as a major cause of death, at least half that died during 1986-98 were first crushed by windblown material. In addition, the largest stem to die (at 61cm gbh) was first knocked over during the 1968 windstorm. In 1998, 14 surviving stems been damaged and two multi-stemmed individuals had lost their largest stem, having been struck by fallen canopy branches/trees snapped during windstorms. In contrast, about twenty stems had vigorous crown growth associated with gaps in the canopy.

Holly had low mortality of large individuals (m<0.22% a^{-1} over the two periods in the Wallace/Backmeroff transects) and most small individuals appear to have survived from 1961-86 (Tables 3.6.5-7). During 1986-98, 35 individuals, all <14cm gbh, died. Although this was probably related to exclusion, a few surviving holly individuals were struck by falling trees/branches and two multi-stemmed individuals had had the largest stem killed off in this way. Some stems survived such damage and continued to grow well, producing new vertical shoots from below the breakage points, whilst others were reduced to lateral crown growth. In 1998, only a small number of released stems were observed. Holly made steady recruitment. The recruits were generally scattered, but the grove at the end of transect I recruited most. Although many recruits were close to existing trees and appeared to be from underground layers, some arose at distance and were probably from seed. By 1998 there were signs that recruitment of holly was declining: the overall number of small individuals had fallen and the number of small recruits only slightly outnumbered the number that died. However, further recruitment seemed likely in four sections with high numbers of low-growing individuals recorded in 1998 (section 1 on transect I, and sections 10, 13 and 14 on transect II).

Hazel mortality rates were highest amongst the main understorey species (Tables 3.6.5-7). Large individuals suffered high mortality and reduction mainly before 1986. After 1986 they recovered slightly as losses decreased and several small individuals developed into or re-established themselves as large individuals. Turnover of small individuals was high: some grew into large individuals, some died, some recruited where large stems died on large individuals, and some recruited from seedlings or layers. Those that died appeared to have been excluded below the oak-dominated canopy, though a few surviving individuals had been crushed by falling canopy debris (this may have contributed to the recorded mortality). Individuals that died before 1986 mainly had <5 stems <18cm gbh recorded or only a single large 28cm gbh stem; but three were larger and had more stems. Over the same period, 23 of the 26 surviving individuals ended up with less live stems, the reduction being greatest on individuals with larger stems at the start (Figure 3.6.8). This reduction was so severe that by 1998 only five individuals remained with >5 live stems ≥5cm gbh. However, several stools had short vigorous basal sprouts present, 30 new stems had grown to ≥5cm gbh since 1986 (Figure 3.6.8), and several small stems had increased substantially in gbh over 1986-98 (large stems invariably grew little).

3.6.2.1.2.5. Stratification in 1998

By 1998, oak accounted for 80% of stems in the canopy in the core woodland transects (Table 3.6.8). Most other remaining canopy stems were birch, but a single beech and Scots pine were also in the canopy. The sub-canopy contained few stems, though amongst these were a few tall holly and rowan. The remaining 88% of stems were in the understorey. Most were of shade-tolerant species: including many holly and rowan stems, plus a few yew. Hazel was restricted to and accounted for 12% of stems in the understorey. Some understorey were smaller, suppressed stems of oak and birch. In fact, almost 80% of birch stems remained in the understorey.

Figure 3.6.8: Change in the number of live stems on hazel individuals in the permanent transects in the core woodland on Clairinsh during 1961-86 (top) and 1986-98 (bottom). The initial size of largest stem on each individual is shown. Larger points represent 2-5 coincident individuals. For 1961, individuals with the largest stem <10cm gbh are shown as 5cm gbh; individuals with 'many' live stems are shown with ten live stems; and those that were parts of 'groups' are shown with three live stems. For 1986 and 1998, only live stems attaining 5cm gbh were counted; and individuals with the largest stem <5cm gbh are shown as 3cm gbh

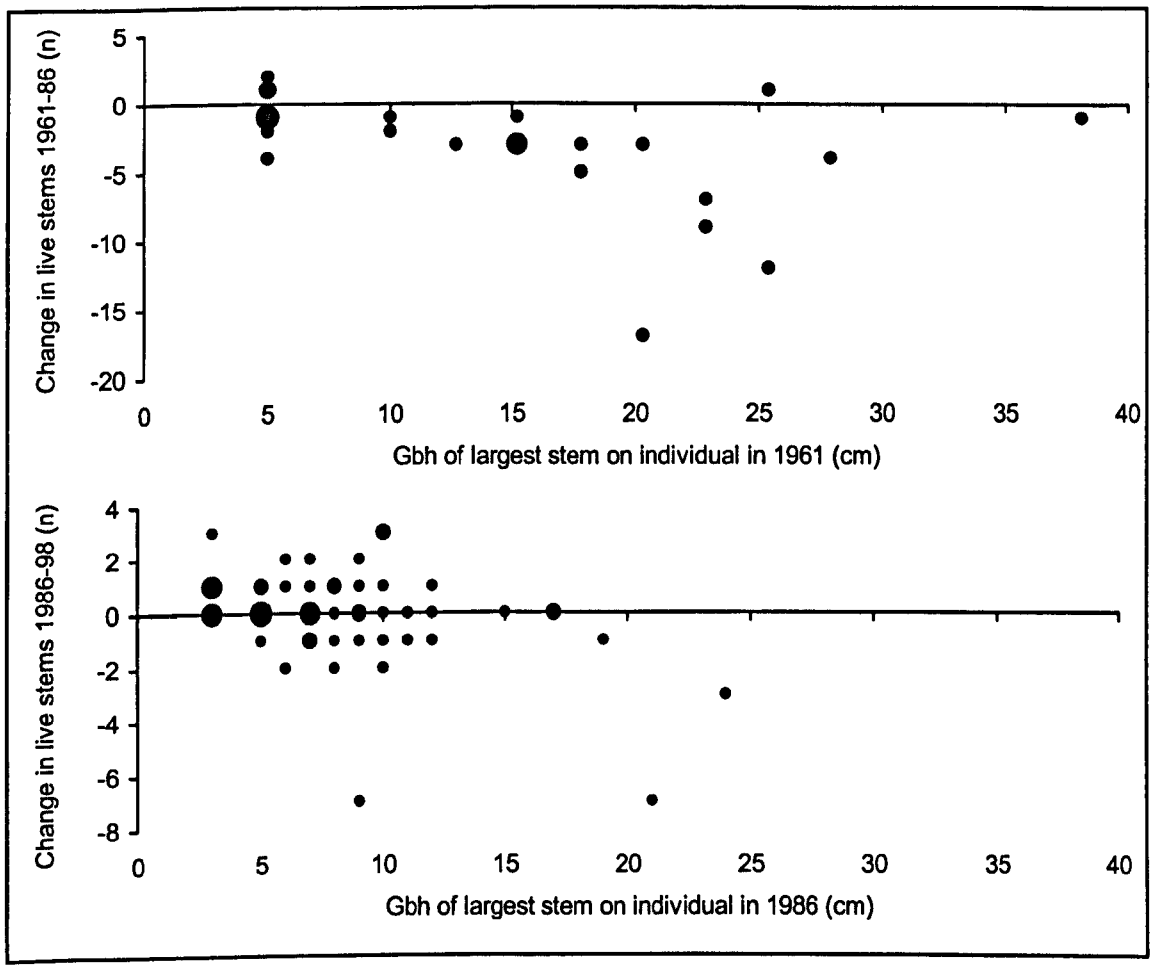


Table 3.6.8: Crown position for all live stems ≥5cm gbh in the permanent transects in the core woodland on Clairinsh in 1998. The table shows the number of stems in each category

	Canopy	Sub-canopy	Understorey
Oak	103	5	47
Birch	24	6	113
Beech	1	1	-
Pine	1	-	-
Holly	-	5	499
Rowan	-	2	293
Hazel	-	-	131
Yew	-	-	25
Alder	-	-	2
Hawthorn	-	-	1
Crab apple	-	-	1
All species	129	19	1112

3.6.2.2. Change in the base-rich marginal woodland

3.6.2.2.1. Stand development before 1961

This woodland type occupied the low-lying ground to the north, between the shoreline and core woodland (Figure 3.6.1). It was crossed by 4-5 sections on transect II, and part was shown on the second stand profile diagram. There were several large oak and one ash present (Table 3.6.9). Together these formed a discontinuous canopy, with the stand being described as 'very open structured, with a broken canopy, no well developed under layer, and much bracken and some bramble'. The sub-canopy/understorey comprised a mixture of alder, ash, birch, blackthorn, broom, guelder rose, hawthorn, hazel, oak and rowan (plus some rose, not included in the analysis). The stand basal area was almost $21 m^2 ha^{-1}$, but the density of large and small individuals was only about half that in the core woodland.

Most of the large canopy trees were 9-14m tall oak, which had presumably been retained in 1913 (Table 3.6.9). None appeared to be have been promoted from coppice stools. The single tree that was cored dated from the early 19th century. The four smaller oak were in the understorey and appeared to be post-1913 recruits. They included a five-stemmed coppice stool and a maiden recruit sited below gaps, both of which had grown vigorously to reach 8m height in 1961. Another maiden had developed less strongly as it was part-shaded by an adjacent large oak. The final small maiden recruit, which had grown little, may well have been a weak basal sprout off one of the larger trees.

The single large, 11m tall, canopy ash also had some 4m tall basal sprouts, indicating it had been promoted from coppice. The other ash individuals at 10-46cm gbh were post-1913 recruits (Table 3.6.9). Most were 3-6m tall, multi-stemmed, coppice individuals growing immediately above the shoreline woodland. A few had seeded in farther down the transect, but only one had developed into a vigorous tree. The only other trees were: (i) two vigorous birch that had grown below gaps to reach 51-61cm gbh and 6-8m height; and (ii)

Table 3.6.9: Basal area, density and size-class distribution for live individuals/stems in the permanent transect in the base-rich marginal woodland on Clairinsh in 1961. The basal area was based on the largest stem on each individual and only included stems ≥10cm gbh. On small individuals the largest stem was <10cm gbh (it was not certain that all of these were recorded)

		Basal area (m^2 ha^{-1})	Large individuals (n ha^{-1})	Small individuals (n ha^{-1})	Gbh size-class (cm) (n stems)								
					<10	10-<30	30-<50	50-<70	70-<90	90-<120	120-<150	150-<200	All sizes
Major species	Oak	15.7	112	11	1	-	2	1	-	1	1	5	11
	Ash	2.8	180	-	-	12	3	-	-	-	1	-	16
Minor species	Hawthorn	0.8	79	22	2	5	1	1	-	-	-	-	9
	Birch	0.6	22	-	-	-	-	2	-	-	-	-	2
	Alder	0.5	11	-	-	-	-	-	1	-	-	-	1
	Rowan	0.4	22	-	-	-	1	1	-	-	-	-	2
	Hazel	<0.1	22	11	1	2	-	-	-	-	-	-	3
	Blackthorn	<0.1	-	45	4	1	-	-	-	-	-	-	5
	Broom	-	-	67	6	-	-	-	-	-	-	-	6
	Guelder rose	-	-	45	4	-	-	-	-	-	-	-	4
	All species	20.9	461	202	18	20	7	5	1	1	2	5	59

an alder at 74cm gbh and 6m height, which was dying back in the shade of a large oak.

Shrubs and smaller trees were also relatively scarce (Table 3.6.9). Hawthorn was most numerous followed by broom, blackthorn, guelder rose, hazel and rowan. Most of these were individuals <20cm gbh and 4m tall, but two hawthorn and two rowan were >45cm gbh and >5m tall and may have been early, fast-grown recruits. Some of the hawthorn combined with the ash coppice stools on the ground immediately above the shoreline to form a low-growing, scrub-like stand with several roses. Most other individuals grew farther down the transect, forming a limited understorey beneath canopy gaps.

3.6.2.2.2. Stand development 1961-98

3.6.2.2.2.1. Canopy gaps

The base-rich marginal woodland remained relatively open. In 1998, canopy gaps covered 32% of transect area (Figure 3.6.7) and there remained much bracken and some bramble (as in 1986). Although some of the gap area in 1998 was where windstorms had broken branches or thrown over canopy trees, the major openings to the north were where the stand had remained open since 1961.

3.6.2.2.2.2. Basal area and density of individuals/stems

The basal area of large individuals within the Wallace transect increased by 39% over 1961-98 to 29m^2 ha^{-1} (Table 3.6.10). In the Backmeroff transect, the basal area for all stems ≥5cm gbh increased to a similar level. The density of large individuals increased in the Wallace transect over 1961-98, but remained static in the Backmeroff transect over 1986-98 (Table 3.6.10). Small individuals fell over 1961-86, but recovered by 1998. Similarly, the density of stems ≥5cm gbh in the Backmeroff transect increased by 29% to 2764ha^{-1} during 1986-98, mainly reflecting an increase in stems 5-<10cm gbh.

Table 3.6.10: Basal area, density and relative importance of live individuals/stems in the permanent transect in the base-rich marginal woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh; small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh; basal area on the Wallace transect was based on the largest stem on each individual and only included stems ≥10cm gbh; basal area on the Backmeroff transect included all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

		Basal area (m^2 ha^{-1})					Large individuals (n ha^{-1})					Small individuals (n ha^{-1})					Relative importance (%)				
		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect	
		1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998
Major species	Oak	15.7	22.0	24.5	19.0	20.0	112	124	124	107	101	11	-	-	-	-	47	52	51	41	39
	Ash	2.8	2.0	2.6	3.2	4.1	180	169	169	173	167	-	22	-	24	-	15	16	12	9	7
Minor species	Hawthorn	0.8	0.6	0.2	1.1	0.8	79	79	56	60	60	22	11	11	54	36	10	8	5	7	5
	Birch	0.6	0.3	0.3	0.4	0.5	22	11	11	30	24	-	-	-	6	-	3	2	1	2	2
	Alder	0.5	0.5	0.1	0.3	<0.1	11	11	11	6	6	-	-	-	-	-	8	5	5	6	7
	Rowan	0.4	0.7	0.8	0.8	1.1	22	11	11	24	24	-	-	-	6	6	3	2	2	3	3
	Hazel	<0.1	0.2	0.2	1.1	1.3	22	34	34	60	60	11	-	22	-	18	3	3	4	5	5
	Blackthorn	<0.1	0.1	0.1	0.4	0.4	11	67	101	119	143	45	56	101	424	472	4	10	15	24	24
	Cedar	-	0.1	0.2	0.1	0.2	-	11	11	6	6	-	-	-	-	-	-	1	1	<1	<1
	Guelder rose	-	<0.1	-	<0.1	<0.1	-	11	-	6	-	34	-	22	54	125	3	1	2	3	5
	Crab apple	-	-	-	<0.1	<0.1	-	-	-	6	6	-	-	-	-	-	-	-	-	<1	<1
	Willow	-	-	-	<0.1	-	-	-	-	6	-	-	-	-	-	-	-	-	-	<1	-
	Holly	-	-	-	<0.1	<0.1	-	-	-	-	-	-	-	11	-	6	-	-	<1	-	<1
	Bird cherry	-	-	-	-	<0.1	-	-	-	-	-	-	-	-	12	12	-	-	-	<1	<1
	Broom	-	-	-	-	-	-	-	-	-	-	67	-	-	6	24	5	-	-	<1	<1
	All species	20.9	26.3	29.0	26.3	28.6	461	528	539	603	603	258	146	270	728	812	100	100	100	100	100

Amongst the species, oak continued to dominate the basal area and changed little in density (Table 3.6.10). It accounted for 75-85%/70-72% of the total basal area within the Wallace/Backmeroff transects and over 1961-98 increased in basal area by 55%. Ash decreased in basal area over 1961-86, but by 1998 had more or less recovered and numbers fell only slightly. Blackthorn increased substantially in density and basal area and became the most numerous species. In addition, western red cedar, hazel, holly and rowan made moderate gains. Guelder rose and broom fluctuated, whilst alder, birch, hawthorn and willow generally declined. Bird cherry and crab apple remained as minor components in the Backmeroff transect.

3.6.2.2.2.3. Survival, mortality and recruitment patterns

The fate and recruitment of individuals/stems is shown in Tables 3.6.11-12. Of 41 large and 23 small individuals recorded on the Wallace transect in 1961, 32 large and 16 small individuals remained alive in 1998. Thus, the overall mortality rates (m) for large and small individuals were 0.68 and 0.99 % a^{-1} respectively. The mortality rate for large individuals increased from 0.63% a^{-1} over 1961-86 (within the Wallace transect) to 1.18-1.39% a^{-1} over 1986-98 (within the Wallace/Backmeroff transects). Over the same periods, the rate for small individuals fell within the Wallace transect (from 2.57% a^{-1} to 0.69% a^{-1}), but within the Backmeroff transect the rate was 3.40% a^{-1} over 1986-98. Of the 16 individuals that died in the Wallace transect over 1961-98, only one was >65cm gbh and 13 were <40cm gbh. Of the 42 individuals that died in the Backmeroff transect over 1986-98, one was >60cm gbh and 39 were <40cm gbh. Recruitment of new individuals increased from 3ha^{-1} over 1961-86 (on the Wallace transect) to 16-35 ha^{-1} over 1986-98 (on the Wallace/Backmeroff transects).

3.6.2.2.2.4. Trends amongst the main species and stratification in 1998

Oak mortality was minimal and no individuals recruited (Tables 3.6.11-12). Although only

Table 3.6.11: Mortality, reduction and recruitment of large live individuals in the permanent transect in the base-rich marginal woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh. The table shows the number of stems in each category

	Wallace transect										Backmeroff transect				
	1961	1961-86				1986	1986-98				1986	1986-98			
	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1961	No. recruited & not recorded in 1961	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1986	No. recruited & not recorded in 1986	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1986	No. recruited & not recorded in 1986
Ash	16	1	-	-	-	15	1	-	1	-	29	3	-	2	-
Oak	10	-	-	1	-	11	-	-	-	-	18	1	-	-	-
Hawthorn	7	2	-	2	-	7	3	-	1	-	10	4	-	4	-
Birch	2	1	-	-	-	1	-	-	-	-	5	1	-	-	-
Rowan	2	1	-	-	-	1	-	-	-	-	4	-	-	-	-
Hazel	2	-	-	1	-	3	-	-	-	-	10	-	-	-	-
Blackthorn	1	-	1	2	4	6	-	1	3	1	20	3	1	7	1
Alder	1	-	-	-	-	1	-	-	-	-	1	-	-	-	-
Cedar	-	-	-	-	1	1	-	-	-	-	1	-	-	-	-
Guelder rose	-	-	-	-	1	1	-	1	-	-	1	-	1	-	-
Crab apple	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Willow	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
All species	41	5	1	6	6	47	4	2	5	1	101	13	2	13	1

Table 3.6.12: Mortality, survival, development and recruitment of small live individuals in the permanent transect in the base-rich marginal woodland on Clairinsh in 1961, 1986 and 1998. Small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh. The table shows the number of stems in each category

	Wallace transect												Backmeroff transect				
	1961	1961-86					1986	1986-98					1986	1986-98			
	No. alive	No. died	No. grown to ≥10cm g.b.h.	No. reduced to <5cm g.b.h.	No. recruited & ≥10cm g.b.h. in 1961	No. recruited & not recorded in 1961	No. alive	No. died	No. grown to ≥10cm g.b.h.	No. recruited & ≥10cm g.b.h in 1986	No. recruited & <5cm g.b.h in 1986	No. recruited & not recorded in 1986	No. alive	No. died	No. grown to & ≥10cm g.b.h.	No. recruited & ≥10cm g.b.h. in 1986	No. recruited & not recorded in 1986
Broom	6	5	-	1	-	-	-	-	-	-	-	-	1	1	-	-	4
Blackthorn	4	1	2	-	1	3	5	-	2	1	2	3	71	18	7	1	32
Guelder rose	3	3	-	-	-	-	-	-	-	1	1	-	9	4	-	1	15
Hawthorn	2	-	2	-	-	1	1	-	1	-	-	1	9	1	4	-	2
Oak	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hazel	1	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	3
Ash	-	-	-	-	-	2	2	1	1	-	-	-	4	2	2	-	-
Bird cherry	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Birch	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-
Rowan	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1
Holly	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
All species	17	9	6	1	1	6	8	1	4	2	3	7	98	28	13	2	58

a few, small, secondary stems were excluded, only one of the smaller trees (located below a large gap in 1961) grew rapidly and accelerated into the canopy by 1998. In addition, a large, 117cm gbh tree was uprooted in the 1968 windstorm and died during 1986-98. This hurricane and later storms left six of the 17 larger surviving trees with notable damage in 1998. These included five canopy trees of 146-232cm gbh that had partial crown loss (one of which had been damaged at the base where a campfire had been burnt), and another 101cm gbh tree that had been relegated to the understorey because the top had been wind-snapped at 3m up. In 1998 oak accounted for most of the taller, canopy trees, and few oak stems persisted in the lower layers (Table 3.6.13).

Table 3.6.13: Crown position for all live stems ≥5cm gbh in the permanent transect in the base-rich marginal woodland on Clairinsh in 1998. The table shows the number of stems in each category

	Canopy	Sub-canopy	Understorey
Oak	13	1	4
Ash	9	1	60
Birch	1	-	5
Hazel	-	-	139
Blackthorn	-	-	119
Hawthorn	-	-	31
Rowan	-	-	21
Guelder rose	-	-	7
Cedar	-	-	4
Alder	-	-	3
Bird cherry	-	-	2
Crab apple	-	-	2
Holly	-	-	1
All species	23	2	367

The single large ash tree was uprooted, possibly in the 1968 windstorm: it was dead by 1986 (Tables 3.6.11-12). Other losses were limited to five small ash individuals of 5-19cm gbh and some stems on coppice stools, all of which were probably excluded. Only two ash saplings recruited, both during 1961-86: one had died by 1998. Although the coppice ash individuals growing adjacent to the shoreline woodland in 1998 were not that tall, the larger stems on these were generally placed in the canopy (Table 3.6.13). In addition, a few stems with vigorous crowns further down the transect were put in the upper layers. These

represented post-1913 recruits, which had sustained rapid growth beyond or in the openings between the large canopy oaks. However, most ash stems grew poorly, remained relatively short, and were placed in the understorey in 1998.

Amongst the other species: (i) one of the two large birch trees died and no recruits established; one surviving tree was in the canopy in 1998, but most were in the understorey; (ii) the largest alder stem died but another smaller stem on the stool grew on; (iii) large individuals of blackthorn had low mortality; many small individuals grew into large ones; and recruitment of small individuals (mainly from suckers during 1986-98) exceeded losses – it became especially abundant in the open-canopied stand immediately above the western shoreline (where it formed a low-growing 'understorey'), though it also remained as a weak understorey below gaps in the stand further down the transect; (iv) hawthorn had several large individuals die and these were only part-replaced by a few small individuals that grew on; (v) guelder rose individuals declined over 1961-86, but they recruited well during 1986-98 to form a low-growing, sprawling mass at 76-83m along the transect – at least part, if not all, of this appeared to be from 'one' individual present that had persisted by repeated suckering; (vi) hazel had all individuals survive to 1998; a few new seedlings recruit; and an increase in both the size of the largest stem and the number of live stems on most individuals – thus, by 1998 some exceptionally large hazel stools had developed; (vii) all the broom individuals present in 1961 died but were replaced by recruits that developed by 1998; and (viii) the single western red cedar recruited during 1961-86, just above the shoreline woodland, and grew vigorously before being felled after the 1998 recording.

3.6.2.3. Change in the base-poor marginal woodland

3.6.2.3.1. Stand development before 1961

This woodland type occupied the low-lying ground to the south of the island (Figure 3.6.1). It was crossed by two sections on transect II and one of the stand profile diagrams from 1961 covered these. Several oak and some alder and birch dominated the stand (Table 3.6.14). They grew over a dense understorey of mainly hazel, holly and rowan, plus some alder, ash, birch, guelder rose and oak. The basal area was around 24m^2 ha^{-1}, and the density of large and small individuals was about twice that in the core woodland.

Table 3.6.14: Basal area, density and size-class distribution for live individuals/stems in the permanent transect in the base-poor marginal woodland on Clairinsh in 1961. The basal area was based on the largest stem on each individual and only included stems ≥10cm gbh. On small individuals the largest stem was <10cm gbh (it was not certain that all of these were recorded)

	Basal area (m^2 ha^{-1})	Large individuals (n ha^{-1})	Small individuals (n ha^{-1})	Gbh size-class (cm) (n stems)					
				<10	10-<30	30-<50	50-<70	70-<150	All sizes
Oak	12.6	200	-	-	2	1	1	4	8
Alder	4.8	325	-	-	5	3	5	-	13
Birch	4.5	250	100	4	6	2	1	1	14
Rowan	1.3	375	150	6	12	3	-	-	21
Hazel	0.6	250	25	4	10	-	-	-	14
Holly	0.3	75	725	29	2	1	-	-	32
Ash	0.1	25	25	2	1	-	-	-	3
Guelder rose	-	-	50	2	-	-	-	-	2
All species	24.2	1500	1075	47	38	10	7	5	107

The four larger-girth canopy oaks (Table 3.6.14) were standards retained in 1913. These had developed into 11-12m tall trees with small to large crowns by 1961. A twin-stemmed coppice individual might also have been retained or it had grown vigorously to 61cm gbh and 10.5m tall. The three smaller individuals (a maiden and two 2-3 stemmed coppice individuals) appeared to be post-1913 recruits: they were all overtopped and suppressed in the understorey in 1961.

All 13 alder present in 1961 (Table 3.6.14) were potentially of coppice origin, though not all the small individuals were multi-stemmed or had additional basal sprouts. By 1961 the six largest individuals had developed into 9-10.5m tall, small-crowned, canopy or sub-canopy trees with one or two main stems: these were clumped between the larger oak. The remaining individuals were <7m tall and suppressed in the understorey.

Birch was about as numerous as alder in 1961, but more individuals were smaller-sized (Table 3.6.14). The largest birch at 112cm gbh had grown into an 11m tall canopy tree: it had an additional 20cm gbh stem suggesting it was from a coppice stool, which may have been stored in 1913. The other individuals appeared to be post-1913 recruits. Most were maidens, but a few were multi-stemmed, coppice individuals. Most had failed to grow above 6m and were overtopped in the understorey. However, two had grown to 9m tall, including a maiden and a twin-stemmed coppice individual below a large gap.

Rowan, holly and hazel were moderately abundant in the understorey in 1961 (Table 3.6.14). The rowan included a group of larger individuals at 20-33cm gbh: most were multi-stemmed and may have been coppiced in 1913. The remaining smaller individuals were mostly single-stemmed: some may have seeded in recently. Most holly individuals were small and appeared to be recent recruits: several were low-layers within a grove around the largest individual, whilst others were at some distance from parent trees. The largest stem on hazel individuals ranged from <10-28cm gbh. Many were multi-stemmed and were probably old coppice individuals. The smallest might have been declining old individuals or more recent recruits.

In addition, ash was a minor constituent with three post-1913 recruits present (Table 3.6.14). Two were from coppice and had three or more stems present, though the largest stem on each was <10cm gbh. The other was a maiden that had grown to 20cm gbh. All

three were <7m tall, overtopped and dying back. Two guelder rose individuals were recorded. Both were <10cm gbh, 3-4m tall, and covered with much honeysuckle. They were likely to be part of a larger cohort that established after 1913.

The canopy was mostly closed and the size-distribution of live individuals (Table 3.6.3) indicated that competitive exclusion had been a major process during the preceding decades. Most small-medium individuals had probably recruited soon after the 1913 felling, but only a few had grown tall and remained vigorous. Many had become overtopped and suppressed, and many small individuals had probably already been excluded. Only shade-tolerant holly and rowan appeared to include some recent recruits.

3.6.2.3.2. Stand development 1961-98

3.6.2.3.2.1. Canopy gaps

The base-poor marginal woodland was partly disturbed by storms during 1961-98. In 1998 21% of the transect area was covered by canopy gaps (Figure 3.6.7). These had been produced by trees windthrown some time ago (potentially in the 1968 windstorm), and also by more recent deterioration or windsnap of canopy trees.

3.6.2.3.2.2. Basal area and density of individuals/stems

The basal area of large individuals within the Wallace transect increased by 46% over 1961-98 to about $35m^2\ ha^{-1}$ (Table 3.6.15). In the Backmeroff transect, the basal area for all stems ≥5cm gbh increased to a similar level. The density of large individuals increased over 1961-98 in the Wallace transect, as it did in the Backmeroff transect over 1986-98. Small individuals on the Wallace transect increased over 1961-86 but by 1998 had fallen. However, they increased slightly over 1986-98 on the Backmeroff transect, as did stems ≥5cm gbh (4325 to $5225ha^{-1}$; mainly reflecting an increase in stems 5-<10cm gbh).

Table 3.6.15: Basal area, density and relative importance of live individuals/stems in the permanent transect in the base-poor marginal woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh; small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh; basal area on the Wallace transect was based on the largest stem on each individual and only included stems ≥10cm gbh; basal area on the Backmeroff transect included all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})					Large individuals (n ha^{-1})					Small individuals (n ha^{-1})					Relative importance (%)				
	Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect	
	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998
Oak	12.6	17.7	18.7	13.9	15.2	200	150	125	125	100	-	-	-	-	-	30	30	29	25	24
Alder	4.8	5.6	3.9	5.9	4.9	325	225	125	150	100	-	25	-	13	-	16	13	8	12	9
Birch	4.5	4.3	4.7	3.4	3.6	250	125	100	150	138	100	50	25	25	13	16	10	9	8	7
Rowan	1.3	1.8	3.5	2.8	3.0	375	375	425	325	313	150	325	200	288	338	13	14	16	13	13
Hazel	0.6	0.4	0.1	0.4	0.3	250	75	75	38	75	25	150	200	513	488	7	4	5	8	8
Holly	0.3	2.4	4.5	3.1	6.0	75	825	1000	1088	1300	725	675	500	813	838	16	28	33	32	38
Ash	0.1	-	-	-	-	25	-	-	-	-	25	-	-	-	-	1	-	-	-	-
Hawthorn	-	0.1	-	<0.1	-	-	25	-	13	-	-	-	-	-	-	-	<1	-	<1	-
Beech	-	-	-	-	<0.1	-	-	-	-	-	-	-	25	-	13	-	-	<1	-	<1
Guelder rose	-	-	-	-	-	-	-	-	-	-	50	-	-	-	-	1	-	-	-	-
All species	24.2	32.2	35.4	29.5	33.0	1500	1800	1850	1888	2025	1075	1225	950	1650	1688	100	100	100	100	100

Amongst the species, oak continued to account for much of the basal area despite declining in density (Table 3.6.15). It accounted for 52-55%/46-47% of the total basal area within the Wallace/Backmeroff transect and over 1961-98 increased in basal area by 48%. Alder increased in basal area over 1961-86, but over 1986-8 it declined by 18-30% on the two transects. Birch basal area did the opposite and overall changed little. The number of individuals of both alder and birch declined progressively. Holly increased greatly in basal area and density, whilst rowan made more moderate gains. In contrast, hazel generally declined, though small hazel individuals increased. In addition, ash and guelder rose died out by 1986, a single hawthorn recruited by 1986 but had died by 1998, and a single beech recruited by 1998.

3.6.2.3.2.3. Survival, mortality and recruitment patterns

The fate and recruitment of individuals/stems is shown in Tables 3.6.16-17. Of 60 large and 47 small individuals recorded on the Wallace transect in 1961, 34 large and 40 small individuals remained alive in 1998. Thus, the overall mortality rates (m) for large and small individuals were 01.54 and 0.44% a^{-1} respectively. The mortality rate for large individuals decreased from 1.71% a^{-1} over 1961-86 (within the Wallace transect) to 0.84-1.29% a^{-1} over 1986-98 (within the Wallace/Backmeroff transects). Over the same periods, the rate for small individuals rose from 1.06% a^{-1} to 1.27-1.47% a^{-1}. Of the 30 individuals that died in the Wallace transect over 1961-98, all were <60cm gbh and 26 were <30cm gbh. Of the 26 individuals that died in the Backmeroff transect over 1986-98, all were <70cm gbh and 22 were <30cm gbh. Recruitment of new individuals went from 45ha^{-1} over 1961-86 (on the Wallace transect) to 20-46ha^{-1} over 1986-98 (on the Wallace/Backmeroff transects).

3.6.2.3.2.4. Trends amongst the main species and stratification in 1998

All large oak trees survived and in 1998 these accounted for half of all canopy stems

Table 3.6.16: Mortality, reduction and recruitment of large live individuals in the permanent transect in the base-poor marginal woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh. The table shows the number of stems in each category

	Wallace transect										Backmeroff transect			
	1961	1961-86				1986	1986-98				1986	1986-98		
	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1961	No. recruited & not recorded in 1961	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1961 & 1986	No. recruited & <10cm g.b.h. in 1986	No. alive	No. died	No. reduced to <10cm g.b.h.	No. recruited & <10cm g.b.h. in 1986
Rowan	15	1	1	2	-	15	-	1	1	2	26	2	2	3
Alder	13	3	1	-	-	9	4	-	-	-	12	4	-	-
Birch	10	5	-	-	-	5	1	-	-	-	12	1	-	-
Hazel	10	3	4	-	-	3	1	-	1	-	3	1	-	4
Oak	8	2	-	-	-	6	1	-	-	-	10	2	-	-
Holly	3	-	-	24	6	33	-	1	-	8	87	-	1	18
Ash	1	1	-	-	-	-	-	-	-	-	-	-	-	-
Hawthorn	-	-	-	-	1	1	1	-	-	-	1	1	-	-
All species	60	15	6	26	7	72	8	2	2	10	151	11	3	25

Table 3.6.17: Mortality, survival, development and recruitment of small live individuals in the permanent transect in the base-poor marginal woodland on Clairinsh in 1961, 1986 and 1998. Small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh. The table shows the number of stems in each category

	Wallace transect														Backmeroff transect				
	1961	1961-86						1986	1986-98						1986	1986-98			
	No. alive	No. died	No. grown to ≥10cm g.b.h.	No. reduced to <5cm g.b.h.	No. recruited & ≥10cm g.b.h. in 1961	No recruited <5cm g.b.h in 1961	No. recruited & not recorded in 1961	No. alive	No. died	No. grown to ≥10cm g.b.h.	No. reduced to <5cm g.b.h.	No. recruited & ≥10cm g.b.h	No. recruited & <5cm g.b.h in 1986	No. recruited & not recordedi n 1986	No. alive	No. died	No. grown to & ≥10cm g.b.h.	No. recruited & ≥10cm g.b.h. in 1986	No. recruited & not recorded in 1986
Holly	29	-	24	1	-	-	23	27	2	8	-	1	2	1	65	2	18	1	21
Rowan	6	-	2	-	-	-	9	13	1	3	1	-	-	-	23	5	3	2	10
Birch	4	3	-	-	-	1	1	3	1	-	-	-	-	-	2	1	-	-	-
Hazel	4	-	-	3	3	-	4	8	1	1	1	-	3	-	41	9	4	-	11
Ash	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Guelder rose	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alder	-	-	-	-	1	-	-	1	1	-	-	-	-	-	1	1	-	-	-
Beech	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-
All species	47	7	26	4	4	1	37	52	6	12	2	1	5	2	132	18	25	4	42

(Tables 3.6.16-18). Mortality was restricted to four smaller trees that were excluded in shade: a maiden and three coppice individuals sized 15-27cm gbh. The single surviving understorey stem changed little in gbh and had been part-broken by a fallen oak top by 1998. Of the eight surviving canopy stems, four had lost parts of their crowns during windstorms (several of which were sprouting strongly below the breakage points), and another had major crown die back (for which there was no obvious cause, though it had not changed in gbh since 1986). No oak recruited during 1961-98.

Table 3.6.18: Crown position for all live stems ≥5cm gbh in the permanent transect in the base-poor marginal woodland on Clairinsh in 1998. The table shows the number of stems in a particular crown position

	Canopy	Sub-canopy	Understorey
Oak	8	-	1
Alder	6	-	12
Birch	2	2	14
Holly	-	-	261
Rowan	-	-	66
Hazel	-	-	45
Beech	-	-	1
All species	16	2	400

Alder lost eight of 25 individuals recorded in 1961 (Tables 3.6.16-17), and six of the eight recorded in 1998 had only one surviving main stem. Those that died were either small gbh understorey individuals or medium gbh sub-canopy individuals in 1961, which failed standing or probably did so. Although five individuals had stems in the canopy in 1998 (including one with two canopy stems), all other stems were in the understorey (Table 3.6.18). Even those in the canopy grew poorly. No alder recruited during 1961-98.

Birch mortality was high (Tables 3.6.16-17) and included nine individuals <23cm gbh and one at 43cm gbh (which was broken in 1961). All appeared to have been excluded. Only two birch stems remained in the canopy in 1998 (Table 3.6.18). Most others were in the understorey. A few trees appeared to have been released into growth below gaps by 1998,

including one that grew rapidly during 1986-98. A single birch recruited during 1961-86 (though this was probably present and small in 1961), but by 1998 it had died.

Large rowan suffered low mortality and overall only eight rowan individuals died (Tables 3.6.16-17). Seven were sized <5-13cm gbh and were probably excluded, whilst the other at 22cm gbh was struck by a fallen canopy bough. Records of survivors in 1998 showed that four others stems had suffered damage from falling canopy boughs. All stems in 1998 were in the understorey (Table 3.6.18), but many were steadily growing upwards and some had been released into growth below canopy gaps, including two that had increased rapidly in gbh. In contrast, stems that been damaged by falling boughs grew slowly. A moderate number of seedlings recruited during 1961-98, but there were few established seedlings <1.3m tall in 1998, suggesting further recruitment could be limited.

Despite problems in reconstructing the 1961 holly population, changes to 1998 indicated that holly had developed strongly in the understorey (Tables 3.6.16-18). Throughout, mortality remained minimal and regeneration substantial. Many recruits were low-layers close to existing holly individuals. Despite these advances, in 1998 only one established holly seedling and one layering stem looked set to recruit within the next few years. The few larger holly stems in 1998 that had suffered damage from falling canopy boughs had responded by developing vigorous crown shoots and, along with several other stems, appeared to have been released into growth below the opened canopy.

Many large hazel individuals died or declined (i.e., the largest stem died and/or the number of live stems decreased), particularly during 1961-86. After 1986, the population was dominated by small individuals with few live stems, but turnover of these was high as numerous new seedlings recruited and almost an equal number died off. During 1986-98 19 new subsidiary stems grew to ≥5cm gbh, and in 1998 several stools had other vigorous

basal sprouts present and appeared to be growing well below the now broken canopy. Nevertheless, only three individuals had more than five live stems ≥5cm gbh and the largest stem was ≥10cm gbh on only six individuals. Although canopy shading had clearly debilitated hazel, fallen canopy branches crushed some individuals/stems and a few certainly died after this.

Amongst the other species: (i) all the ash and guelder rose had died by 1986 and no new recruits developed; (ii) the single hawthorn recruit recorded in 1986 (which was probably too small to have been included in 1961), had been snapped off by a fallen canopy bough and died by 1998; (iii) a single vigorous beech sapling had recruited by 1998, though this had lost its original leader (probably because it had been hit), and another beech seedling <1.3m tall was also recorded (though this was in poor condition).

3.6.2.4. Change in the shoreline shingle woodland

This woodland type included areas growing on exposed shingle beach at the loch edge. It was sampled at the north end of the island by transect II (Figure 3.6.1). The basal area and density of individuals recorded in 1961, 1986 and 1998 are summarised in Table 3.6.19. The stand in 1961 differed from the core and marginal woodland: the basal area and density of large individuals was low; no large trees were present; smaller individuals were frequent; and many individuals were multi-stemmed and described as 'bushy'. The seven largest individuals included four ash and an alder, birch and hawthorn. The largest stem on each was only 23-48cm gbh and 4-5m in height. The smaller individuals were mainly of alder, guelder rose and willow, together with some ash, hawthorn and rowan (plus some rose not included in the analysis). The species occurred along a gradient: alder, birch and willow were most abundant closest to the shore, whilst on the higher ground the mixture was similar to the base-rich marginal woodland with mainly ash, guelder rose, hawthorn and rowan (plus some blackthorn, broom, crab apple and oak recorded in 1986/98).

Table 3.6.19: Basal area, density and relative importance of live individuals/stems in the permanent transect in the shoreline shingle woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh; small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh; basal area on the Wallace transect was based on the largest stem on each individual and only included stems ≥10cm gbh; basal area on the Backmeroff transect included all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})					Large individuals (n ha^{-1})					Small individuals (n ha^{-1})					Relative importance (%)				
	Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect	
	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998
Ash	3.4	4.7	5.4	5.2	6.4	400	600	500	426	393	100	-	100	-	33	34	24	26	17	17
Alder	1.9	4.0	4.5	3.7	4.1	100	400	400	295	230	500	-	300	33	197	26	19	25	12	14
Birch	1.0	2.9	-	6.9	6.7	100	100	-	98	66	-	-	-	-	-	9	10	-	14	11
Hawthorn	0.9	1.6	1.7	0.7	0.7	200	200	200	98	131	-	-	-	66	33	11	8	8	4	4
Guelder rose	0.1	0.2	-	0.5	0.5	100	200	-	98	131	300	100	100	361	295	10	6	2	9	8
Willow	-	3.1	4.6	6.7	10.9	-	1000	1000	623	623	400	100	100	295	230	9	28	31	28	31
Rowan	-	0.4	0.5	0.1	0.2	-	100	100	33	33	100	-	-	-	-	2	3	3	<1	<1
Crab apple	-	-	-	1.0	1.1	-	-	-	33	33	-	100	100	33	33	-	2	2	3	3
Broom	-	-	-	-	-	-	-	-	-	-	-	-	200	33	98	-	-	3	<1	2
Blackthorn	-	-	-	1.5	0.1	-	-	-	98	33	-	-	-	262	164	-	-	-	9	4
Oak	-	-	-	1.4	2.8	-	-	-	33	33	-	-	-	33	33	-	-	-	4	5
All species	7.3	16.9	16.7	27.8	33.4	900	2600	2200	1836	1705	1400	300	900	1115	1115	100	100	100	100	100

During 1961-98 the stand developed considerably. By 1986 the basal area had more than doubled and the density of larger individuals had almost trebled. However, smaller individuals declined. Although the basal area did not increase on the Wallace transect over 1986-98, it did on the Backmeroff transect to reach about $33m^2\ ha^{-1}$. Large individuals showed a slight decline over this period, whilst small individuals increased on the Wallace transect and remained static on the Backmeroff transect.

Willow developed strongly on the ground immediately adjacent to the shore. Most of the willow bushes present in 1961 grew into large, multi-stemmed individuals. Several had collapsed, become covered by washed-up shingle, and then rooted and grown many vigorous shoots. It was difficult to decide which stems belong to which individuals in the ensuing mass. The willows had helped reduce erosion and the shingle beach appeared to have extended a few metres into the loch over 1961-98. Alder developed well during 1961-86, but gains thereafter were moderate. It appeared to have lost out in competition with birch and ash: several smaller individuals/stems had died and many of the survivors grew little in gbh during 1986-98. The three alder that recruited did so after 1986, but these were all weak growth off old stumps or horizontal stems. Birch changed little overall, with losses due to thinning being cancelled out by the growth of surviving stems. The higher basal area in the Backmeroff transect was because the wider transect included a large multi-stemmed birch stool. Ash remained dominant on the higher ground. Although there was no suggestion of post-1961 recruitment, ash losses were few and small-sized, and the survivors grew well. The largest of the two oaks recorded in the Backmeroff transect grew vigorously over 1986-98. In addition, seven other minor species managed to survive or developed below the low-growing, open canopy.

3.6.2.5. Change in the shoreline shelf woodland

This woodland type runs around much of the island and comprises: (i) a platform shelf adjacent to the loch; and (ii) a marginal bank that defines the boundary between this and the core woodland. It was sampled at the start and end of transect I, and at the end of transect II (Figure 3.6.1). At the end of transect I the platform shelf was crossed, though the strip covered was only about 5m wide and stopped 6m short of the loch edge. Only a very small strip at the end of transect II was crossed. The platform shelf crossed at the start of transect I was not re-recorded in 1986 or 1998, so this was excluded from the analysis. However, trees growing on the marginal bank were sampled at all three locations.

The basal area and density of individuals recorded in 1961, 1986 and 1998 are summarised in Table 3.6.20. The marginal bank was similar in composition to the core woodland. It included oak, birch, rowan, holly and hazel, with some large oak standards, a large oak pollard, and some oak coppice stools. Species that extended down the shelf included alder, ash, birch and hawthorn, though bird cherry, broom, guelder rose, hornbeam, oak, sycamore and willow grow elsewhere on the shelf.

The basal area and density of both large and small individuals was high in 1961. Changes over 1961-98 were limited: the canopy remained largely closed; smaller individuals thinned out, but the basal area increased; and there was virtually no recruitment. Oak remained dominant on the marginal bank with all larger oak surviving. Rowan and holly developed in the understorey, but hazel died out with the original stools being undermined and washed away by wave action. Indeed, the marginal bank was eroded wherever tree roots were sparse; at the end of transect II the bank shifted up to 3m inland; and several smaller oak, rowan and holly individuals were consequently toppled. On the platform shelf, birch survived best but grew slowly, ash, rowan and hawthorn remained restricted to the understorey, and alder and oak were excluded. A sycamore positioned just outside the

Table 3.6.20: Basal area, density and relative importance of live individuals/stems in the permanent transect in the shoreline shelf woodland on Clairinsh in 1961, 1986 and 1998. Large individuals on both transects included those with the largest stem ≥10cm gbh; small individuals on the Wallace transect included those with the largest stem <10cm gbh in 1961 (it was not certain that all these were recorded) and those between 5-<10cm gbh in 1986 and 1998; small individuals on the Backmeroff transect included those ≥1.3m in height and with the largest stem <10cm gbh; basal area on the Wallace transect was based on the largest stem on each individual and only included stems ≥10cm gbh; basal area on the Backmeroff transect included all stems ≥5cm gbh. Relative importance = [% total basal area + % all stems]÷2

	Basal area (m^2 ha^{-1})					Large individuals (n ha^{-1})					Small individuals (n ha^{-1})					Relative importance (%)				
	Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect		Wallace transect			Backmeroff transect	
	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998	1961	1986	1998	1986	1998
Oak	54.8	80.7	85.7	45.5	47.2	588	353	353	537	390	-	-	-	-	-	58	55	55	58	58
Birch	3.9	7.5	7.7	3.6	3.2	471	471	471	195	195	118	-	-	-	-	18	18	19	9	10
Rowan	1.7	1.8	2.0	2.3	2.3	235	235	235	293	244	-	-	-	49	49	7	8	9	11	13
Alder	1.2	-	-	-	-	118	-	-	-	-	-	-	-	-	-	4	-	-	-	-
Hawthorn	0.9	-	-	<0.1	0.1	118	-	-	49	49	-	118	-	49	-	4	4	-	3	2
Ash	0.4	0.3	0.4	0.2	0.2	118	118	118	49	49	-	-	-	-	-	3	4	4	1	2
Hazel	0.2	-	-	0.1	-	118	-	-	-	-	-	-	-	293	49	3	-	-	8	2
Holly	0.1	1.1	1.9	0.7	1.8	118	235	353	244	293	-	118	-	98	-	3	11	12	10	13
All species	63.1	91.4	97.6	52.4	54.8	1882	1412	1529	1366	1220	2000	1647	1529	1854	1317	100	100	100	100	100

end of transect II, survived but grew little. Trees on the platform shelf also suffered from the erosion around their roots and by 1998 several surviving individuals were leaning over.

3.6.2.6. Stem growth amongst the main species

The gbh/basal area increment analysis included only the main species and combined stems from all parts of the transects. Three aspects were examined: (i) the relationship between the increment rate and initial size of stems over 1961-98 and 1986-98; (ii) the increment rate for stems in 1961-86 against 1986-98; and (iii) the increment rate for stems in different crown position categories in 1998.

All of the main species had at least one significant regression relationship between the increment and initial size of stems. However, in a few cases the regression was not significant and several, which were significant, accounted for only a small amount of the total variation (Table 3.6.21a/b, Figures 3.6.9-12). Most regressions based on changes in basal area accounted for far more variation than those based on gbh. Most based on changes over 1986-98 were significant and/or accounted for more variation than those over 1961-98. In most cases the regression lines peaked at the higher end of the initial size range, indicating that larger stems generally increased more than smaller stems. Hazel and alder had the weakest regressions overall, whilst all or some of those for the other species were particularly strong.

Increment rates between 1961-86 and 1986-98 were significantly correlated for oak, birch, rowan and ash, but only the basal area rates were for holly, and none were for hazel or alder (Table 3.6.21c). Despite the correlations, both the gbh/basal area rates for oak and birch and the basal area rates for ash and holly were significantly higher during the first period (Table 3.6.21c).

Table 3.6.21: Results of the stem increment analysis for the main species in the permanent transects on Clairinsh. Figures 3.6.9-12 show the regression relationships as scatter plots. ns = not significant

(a) Regressions comparing gbh increment (inc_{gbh}, cm a^{-1}) against initial gbh (ini_{gbh}, cm)

Species	Period	Regression equation	n	F	P	r^2%
Oak	1961-98	$\log(inc_{gbh+1}) = 0.0005.ini_{gbh} + 0.1490$	91	5.9	0.02	6.2
	1986-98	$\log(inc_{gbh+1}) = -0.0625.ini_{gbh}^2 + 0.2696.ini_{gbh} + 0.0547$	189	12.8	<0.001	12.1
Birch	1961-98	$\log(inc_{gbh+1}) = 0.0015.ini_{gbh} + 0.0474$	44	3.4	0.07	7.6
	1986-98	$\log(inc_{gbh+1}) = 0.1634.\log(inc_{gbh+1})^2 - 0.3356.\log(inc_{gbh+1}) + 0.1952$	153	17.6	<0.001	19.0
Rowan	1961-98	$\log(inc_{gbh+1}) = 0.0003.ini_{gbh}^2 - 0.0098.ini_{gbh} + 0.1735$	50	2.4	0.10	9.3
	1986-98	$\log(inc_{gbh+1}) = 0.0796.\log(inc_{gbh+1}) - 0.0152$	304	21.2	<0.001	6.5
Holly	1961-98	no significant regression	16	-	-	-
	1986-98	$\log(inc_{gbh+1}) = -0.2088.\log(inc_{gbh+1})^2 - 0.7333.\log(inc_{gbh+1}) - 0.4317$	482	107.7	<0.001	31.0
Ash	1961-98	no significant regression	18	-	-	-
	1986-98	$\log(inc_{gbh+1}) = 0.1935.\log(inc_{gbh+1}) - 0.1469$	84	37.4	<0.001	31.3
Hazel	1961-98	not tested	7	-	-	-
	1986-98	no significant regression	198	-	ns	-
Alder	1961-98	not tested	6	-	-	-
	1986-98	no significant regression	31	-	ns	-

(b) Regressions comparing basal area increment (inc_{ba}, cm^2 a^{-1}) against initial basal area (ini_{ba}, cm^2)

Species	Date	Regression equation	n	F	P	r^2%
Oak	1961-98	$\log(inc_{ba+1}) = -0.0311.\log(ini_{ba+1}^2) + 0.7011.\log(ini_{ba+1}) - 0.7158$	90	32.6	<0.001	42.9
	1986-98	$\log(inc_{ba+1}) = 0.4766.\log(ini_{ba+1}) - 0.5245$	186	173.3	<0.001	48.5
Birch	1961-98	$\log(inc_{ba+1}) = 0.4020.\log(ini_{ba+1}^2) - 1.1092.\log(ini_{ba+1}) + 0.9413$	44	8.9	<0.001	30.4
	1986-98	$\log(inc_{ba+1}) = 0.3223.\log(ini_{ba+1}^2) - 0.7971.\log(ini_{ba+1}) + 0.5296$	152	43.1	<0.001	36.6
Rowan	1961-98	$\log(inc_{ba+1}) = 0.0028.ini_{ba} + 0.1552$	50	7.8	0.007	14.0
	1986-98	$\log(inc_{ba+1}) = 0.1579.\log(ini_{ba+1}^2) - 0.1847.\log(ini_{ba+1}) + 0.1369$	304	73.1	<0.001	32.8
Holly	1961-98	$\log(inc_{ba+1}) = 0.3162.\log(ini_{ba+1}) + 0.0519$	16	7.4	0.02	34.5
	1986-98	$\log(inc_{ba+1}) = -0.0449.\log(ini_{ba+1}^2) + 0.5267.\log(ini_{ba+1}) - 0.2611$	482	285.7	<0.001	54.4
Ash	1961-98	$\log(inc_{ba+1}) = 0.0021.ini_{ba} + 0.3757$	18	4.1	0.06	20.2
	1986-98	$\log(inc_{ba+1}) = 0.2137.\log(ini_{ba+1}^2) - 0.2068.\log(ini_{ba+1}) + 0.0929$	84	95.2	<0.001	70.2
Hazel	1961-98	not tested	7	-	-	-
	1986-98	$\log(inc_{ba+1}) = 0.1176.\log(ini_{ba+1}^2) - 0.1263.\log(ini_{ba+1}) + 0.1107$	198	10.6	<0.001	9.8
Alder	1961-98	not tested	6	-	-	-
	1986-98	$\log(inc_{ba+1}) = 0.1686.\log(ini_{ba+1}) + 0.0181$	31	8.5	0.007	22.6

(c) Comparison of gbh increment rates (cm a^{-1}) and basal area increment rates (cm^2 a^{-1}) over 1961-86 and 1986-98 for individual stems and for all stems combined

			Rank correlation between individual stem rates		Paired-sample t-test comparisons of average rate for all stems			
	Species	n	r_s	P	1961-86 rate	1986-98 rate	t	P
Gbh increment rates	Oak	89	0.70	<0.001	0.75	0.51	4.7	<0.001
	Birch	42	0.59	<0.001	0.33	0.23	1.8	0.04
	Ash	18	0.66	<0.005	0.49	0.45	0.6	ns
	Rowan	50	0.51	<0.001	0.23	0.26	0.6	ns
	Holly	15	0.21	ns	0.54	0.64	0.9	ns
	Hazel	7	0.47	ns	0.14	0.04	0.8	ns
	Alder	6	0.34	ns	0.27	0.11	1.3	ns
Basal area increment rates	Oak	89	0.74	<0.001	14.9	11.4	2.8	0.004
	Birch	42	0.64	<0.001	2.9	2.2	1.5	0.08
	Ash	18	0.81	<0.001	2.5	3.1	1.6	0.06
	Rowan	50	0.65	<0.001	1.2	1.4	0.6	ns
	Holly	15	0.51	<0.05	3.6	4.8	1.8	0.05
	Hazel	7	0.54	ns	0.5	0.2	0.9	ns
	Alder	6	0.52	ns	2.5	1.2	1.2	ns

Figure 3.6.9: Relationship between the gbh increment and initial gbh of stems for the main species on Clairinsh over 1961-98. Parameters for the regression lines shown are given in Table 3.6.21. Some symbols represent more than one stem

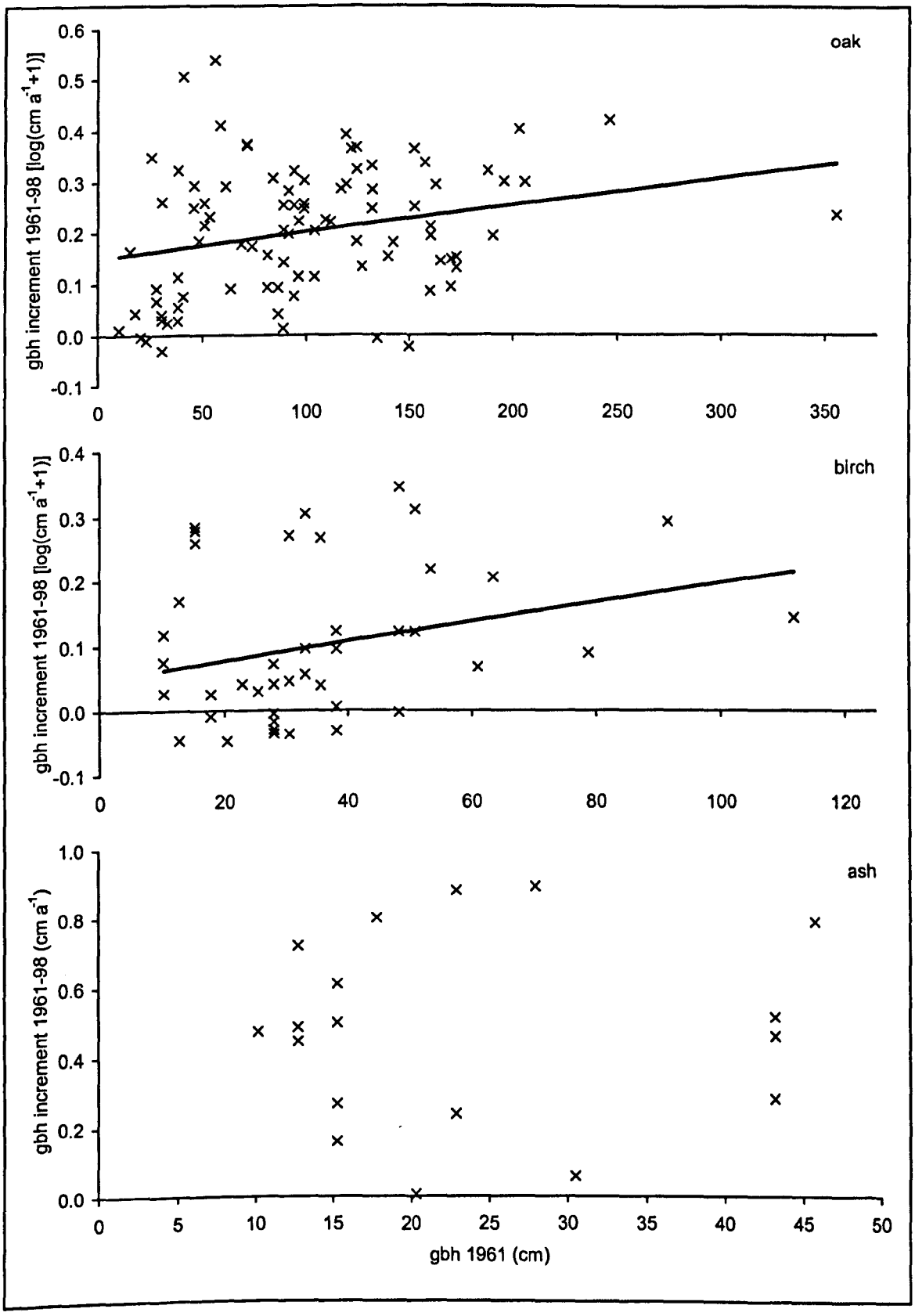


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Figure 3.6.9: continued

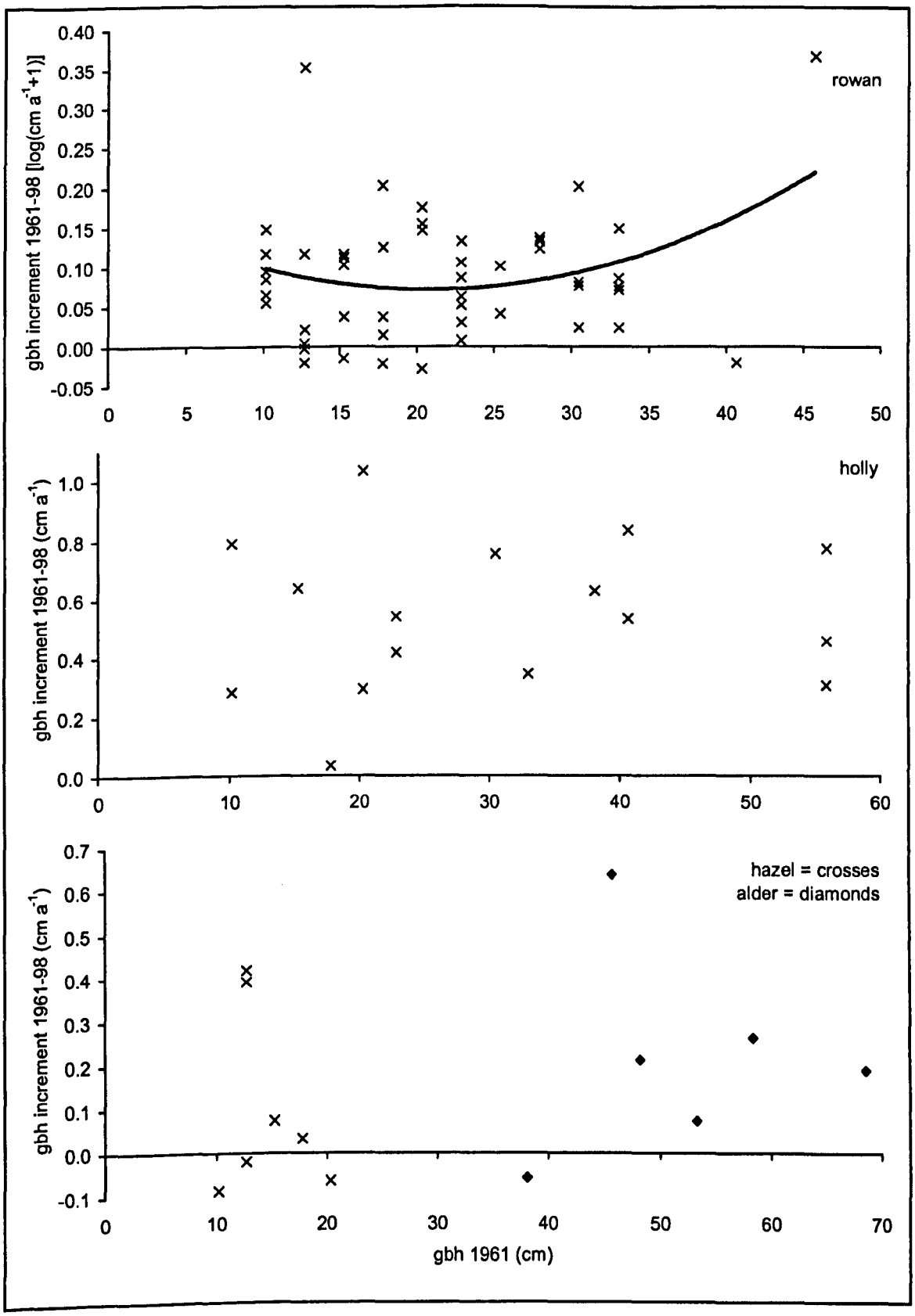

Figure 3.6.10: Relationship between the gbh increment and initial gbh of stems for the main species on Clairinsh over 1986-98. Parameters for the regression lines shown are given in Table 3.6.21. Some symbols represent more than one stem

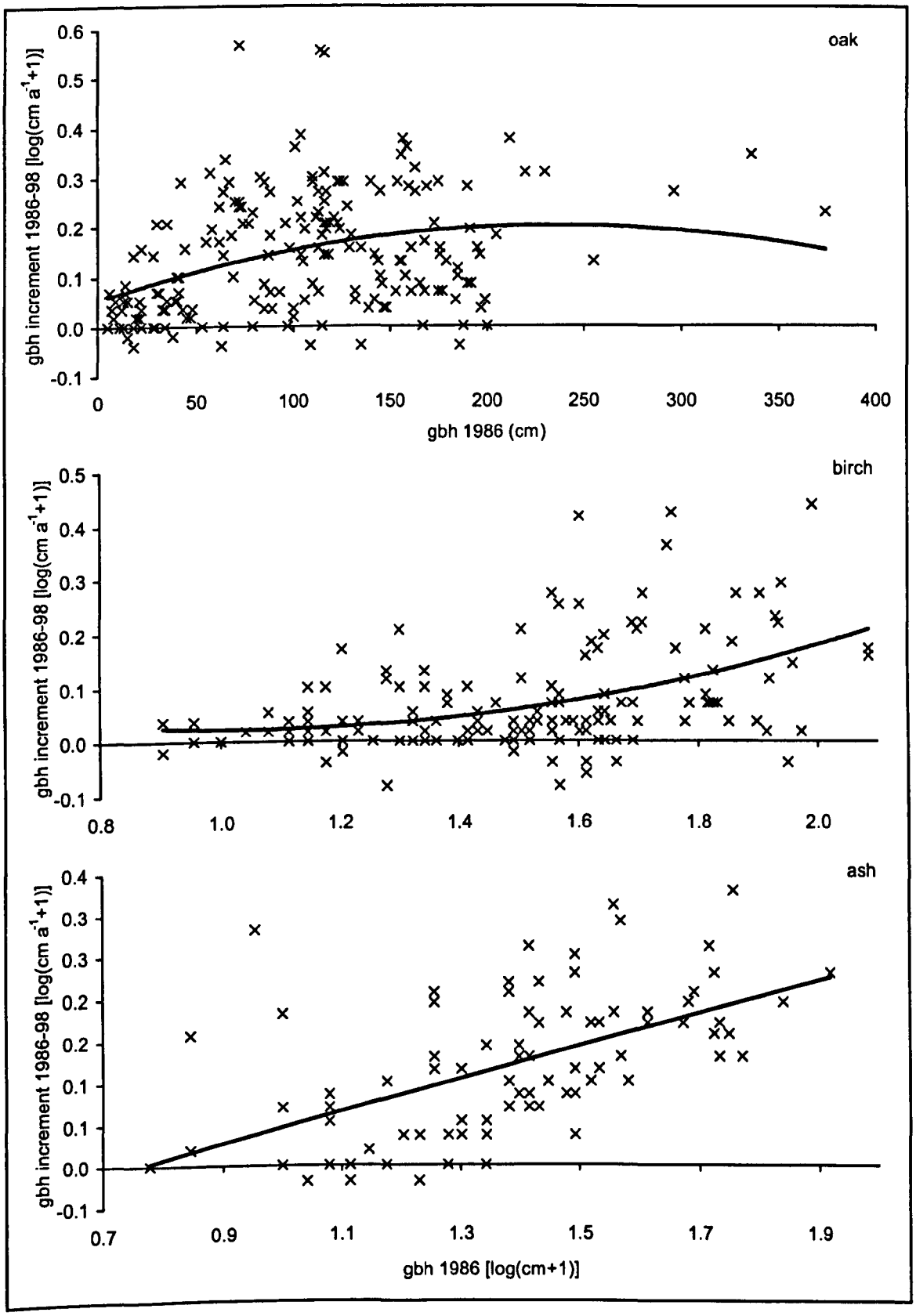

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Figure 3.6.10: continued

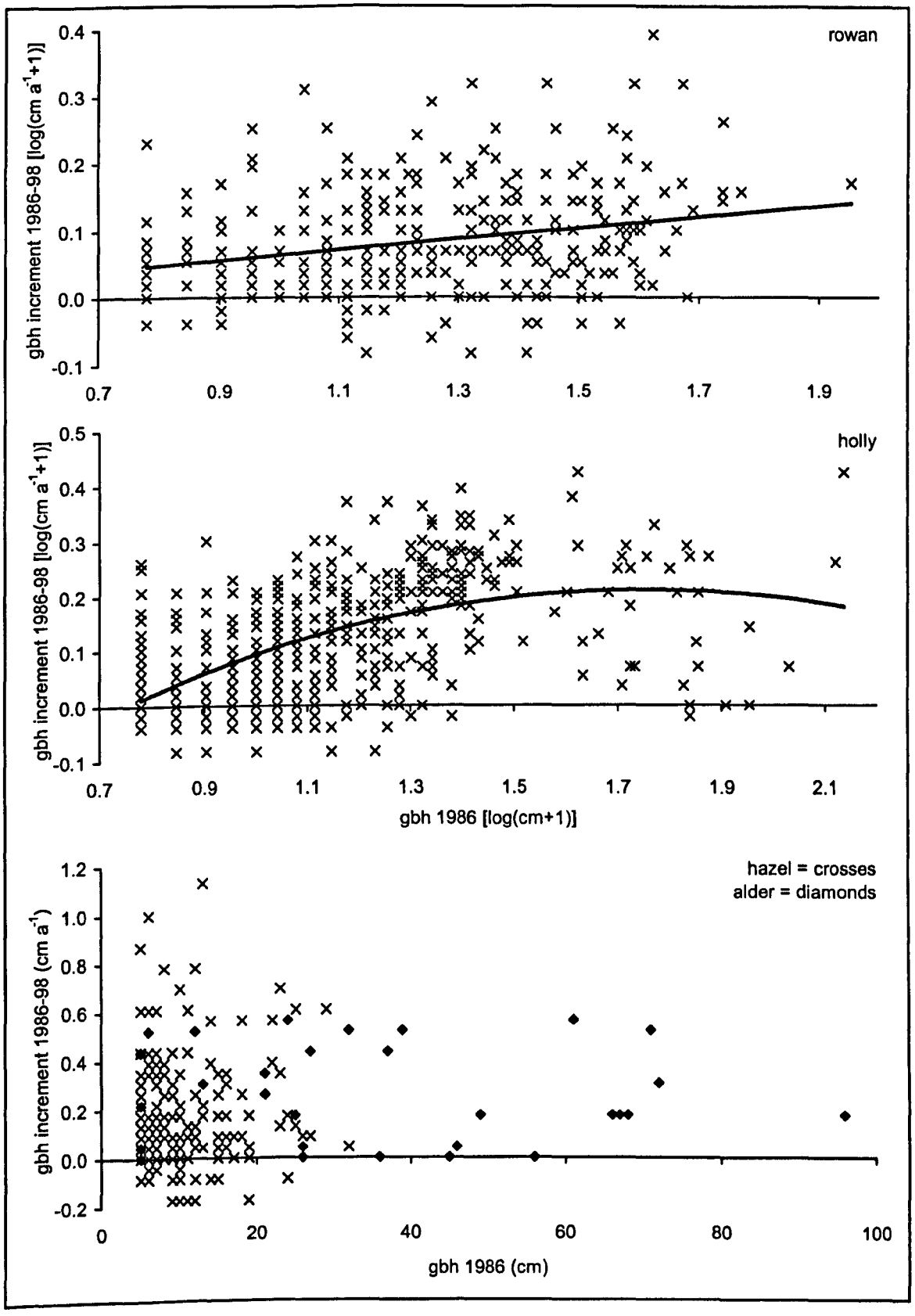

Figure 3.6.11: Relationship between the basal area increment and initial basal area of stems for the main species on Clairinsh over 1961-98. Parameters for the regression lines shown are given in Table 3.6.21. Some symbols represent more than one stem

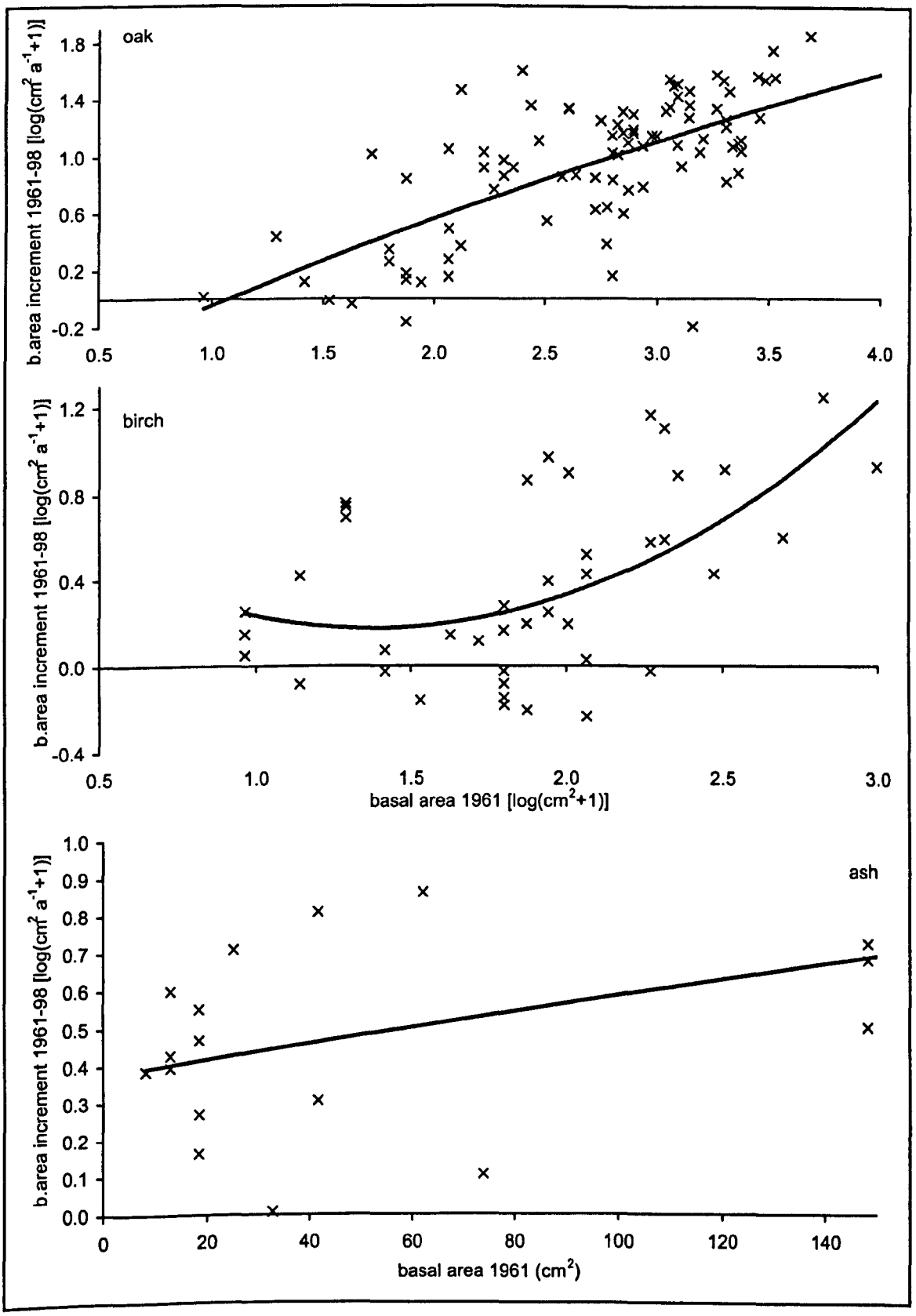

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Figure 3.6.11: continued

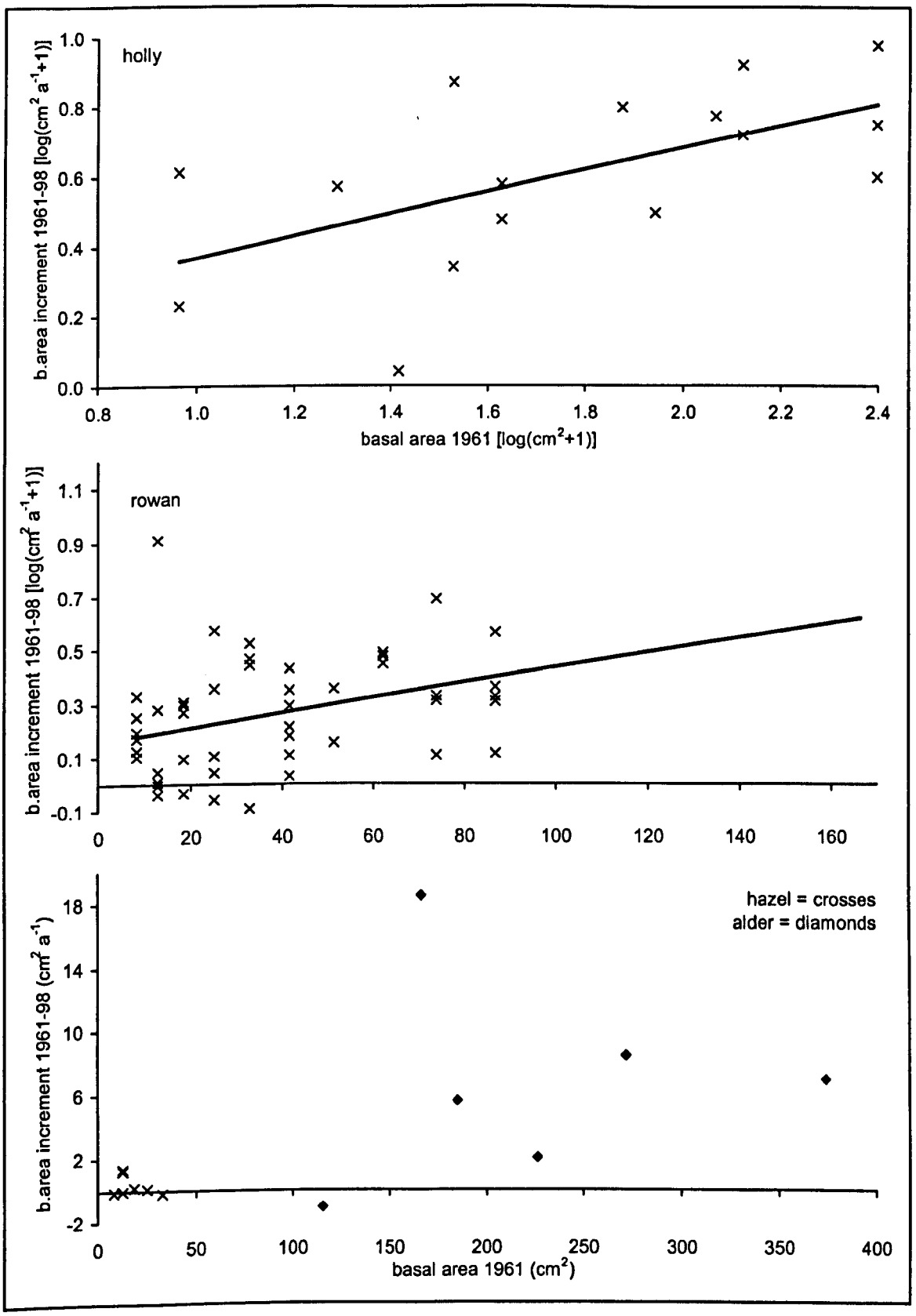

Figure 3.6.12: Relationship between the basal area increment and initial basal area of stems for the main species on Clairinsh over 1986-98. Parameters for the regression lines shown are given in Table 3.6.21. Some symbols represent more than one stem

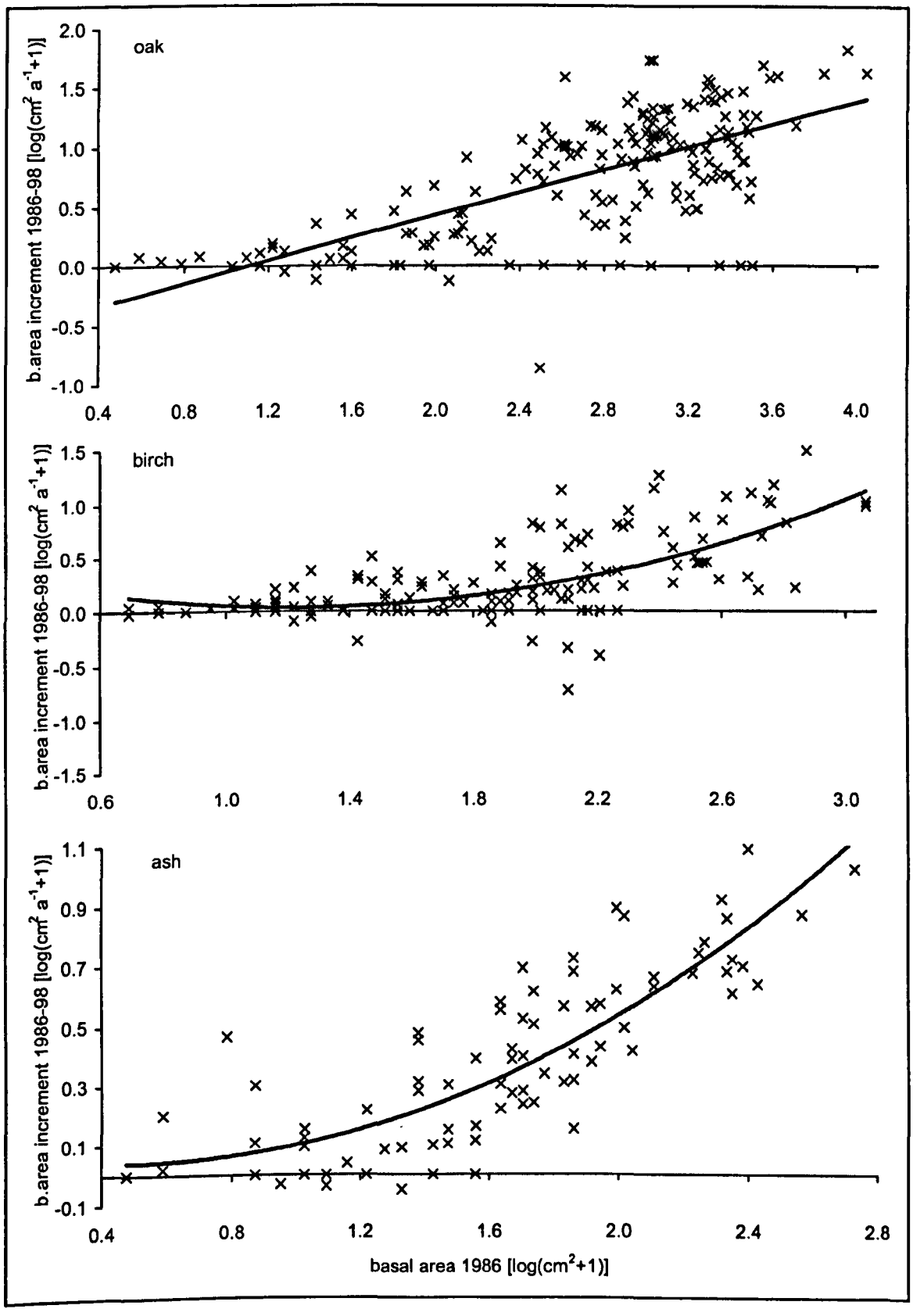

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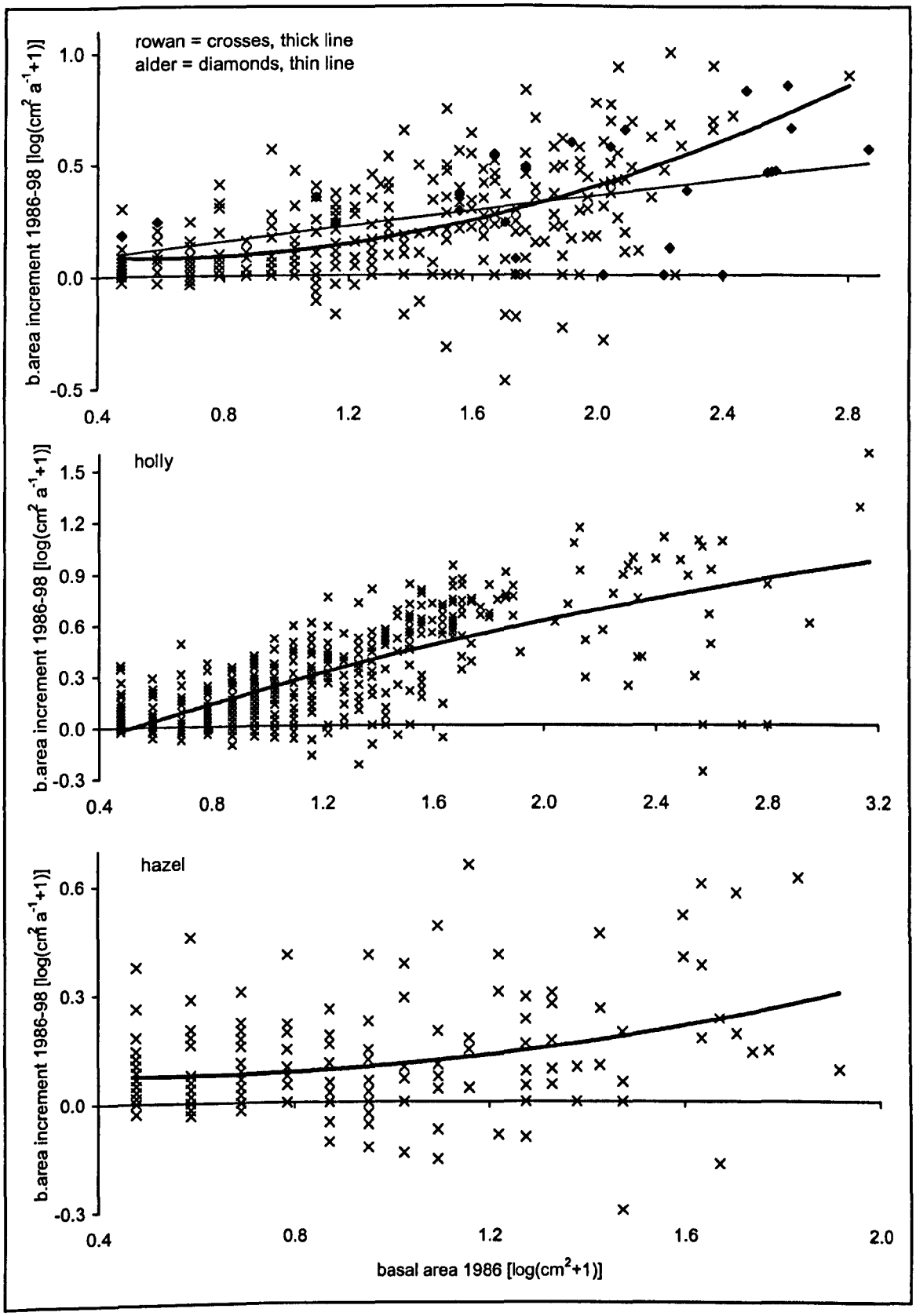
Figure 3.6.12: continued



Stems of oak, birch and ash that ended up in the canopy invariably had higher increments than those that ended up in the sub-canopy or understorey (Table 3.6.22), indicating that shading had strongly affected growth. For alder, such differences were much less distinct.

Table 3.6.22: Comparison of the increment rates over 1961-98 and 1986-98 for stems in different crown position categories in 1998 for the main species in the permanent transects on Clairinsh during. The table shows: (i) the median rate for each category based on changes in stem gbh (cm a^{-1}) and basal area (cm^2 a^{-1}); and (ii) the significance of the difference between each pair of medians based on a Mann-Whitney two-sample rank (U) test (*** = P<0.001, ** = P<0.01, * = P<0.05, ^{ns} = not significant)

(a) Oak	crown position	n	median	comparison
Gbh increment rates 1961-98	canopy	70	0.77	U = 3803***
	sub-canopy or understorey	21	0.10	
Gbh increment rates 1986-98	canopy	130	0.52	U = 14686***
	sub-canopy or understorey	59	0.13	
Basal area increment rates 1961-98	canopy	70	13.13	U = 3803***
	sub-canopy or understorey	21	0.81	
Basal area increment rates 1986-98	canopy	130	9.72	U = 15441***
	sub-canopy or understorey	59	0.46	

(b) Birch	crown position	n	median	comparison
Gbh increment rates 1961-98	canopy	13	0.85	U = 472***
	sub-canopy or understorey	31	0.09	
Gbh increment rates 1986-98	canopy	31	0.52	U = 3936.5***
	sub-canopy or understorey	122	0.04	
Basal area increment rates 1961-98	canopy	13	6.86	U = 486***
	sub-canopy or understorey	31	0.39	
Basal area increment rates 1986-98	canopy	31	5.42	U = 4162***
	sub-canopy or understorey	122	0.22	

(c) Ash	crown position	n	median	comparison
Gbh increment rates 1986-98	canopy	12	0.50	U = 767***
	sub-canopy or understorey	72	0.26	
Basal area increment rates 1986-98	canopy	12	3.74	U = 868***
	sub-canopy or understorey	72	0.95	

(d) Alder	crown position	n	median	comparison
Gbh increment rates 1986-98	canopy	7	0.17	U = 125^{ns}
	sub-canopy or understorey	24	0.20	
Basal area increment rates 1986-98	Canopy	7	2.69	U = 179**
	sub-canopy or understorey	24	0.72	

Most stems attained a gbh increment rate of <0.6cm a^{-1} over 1961-98 and 1986-98, but a minority grew more rapidly (Figures 3.6.9-10, Table 3.6.21a). Although medium and/or larger ash, birch, oak and holly stems tended have grown more in one or both of these periods, the trends were weak. Rather, stems that grew more rapidly (>0.6cm gbh a^{-1}) were generally spread across the size-range for each species. They mainly included: (i) medium-large oak or birch stems with well-developed crowns that mainly ended up in the canopy;

and (ii) medium-small sub-canopy/understorey stems with vigorous and/or released crowns in 1998. Amongst the species, they included: (i) numerous oak from all four woodland types; (ii) some birch, rowan and hazel mainly from the core and base-rich woodland; (iii) many holly mainly from the core and base-poor woodland; (iv) some ash from the base-rich and shoreline woodland; and (iv) an alder from the base-poor woodland.

For all species the basal area increments over 1961-98 and 1986-98 were moderately or strongly related to the initial basal area of stems, with larger and/or medium stems tending to have increased most (Figure 3.6.11-3.6.12, Table 3.6.21b). Species other than oak mostly increased by $<10cm^2\ a^{-1}$, with just a few birch, ash, holly and rowan increasing by more. Oak, however, had many stems increase by this amount. These occurred in all four woodland types and all but one (which grew rapidly to 1986, but then stopped and by 1998 was mostly crown-dead) were canopy trees in 1998 with well-developed, vigorous and/or released crowns. In general, younger canopy oaks grew more than older and some grew to sizes attained by older, but slower-growing trees.

For oak, birch, ash and rowan, both the gbh and basal area increment rates over 1961-86 and 1986-98 were significantly correlated. However, only the basal area rates were correlated for holly, and for hazel and alder neither were correlated strongly (Table 3.6.21c). This indicated that many stems of most species retained the same relative gbh or basal area growth rate over the two periods. Even so, some stems grew more rapidly over 1961-98 or 1986-98. For oak, many stems grew less in 1961-86 than in 1986-98 and the average gbh and basal area increment rates dropped significantly (Table 3.6.21c). Indeed, 21 oak stems from across the size range and all woodland types had the gbh and/or basal area increment fall by $>0.5cm\ a^{-1}$ or $>10cm^2\ a^{-1}$ (compared to only three that increased by this amount). Although on several trees this could be linked to them being described as suppressed/checked or with wind damage or crown die back, many remained with

reasonably vigorous crowns in the canopy. For birch, the average gbh increment rates were significantly higher in 1961-86 than in 1986-98, whilst the basal area were nearly so (Table 3.6.21c). Only four birch stems from the core and shoreline woodland declined in increment by >0.5cm gbh a^{-1} (and none increased by this amount). No other species showed a strongly significant change in the average gbh or basal area increment rate. Even so, a few stems grew more rapidly in one or other period, including two rowan, two hazel, one alder and one holly stem that declined in increment by >0.5cm gbh a^{-1}, and two holly, one rowan and one hazel stem that increased by this amount.

3.6.2.7. Deadwood during 1986-98

3.6.2.7.1. Changes in snags

Only four snags were recorded in 1961: all had collapsed by 1986. Changes in snag basal area and density from 1986 to 1998 are shown in Table 3.6.22. Many species formed snags. However, few snags attained 50cm gbh and therefore few species contributed much to the total basal area. The main species involved was oak, though hazel and birch snags were relatively numerous in 1986. Changes in the basal and density were small, and oak remained most important at both dates. Snags of hazel and birch snags declined.

The turnover of snags between 1986 and 1998 was substantial (Table 3.6.23). Only 11% from 1986 remained standing in 1998, and of the snags present in 1998 only 14% had stood for over ten years. Percentage survival was: (i) higher for snags of ≥50cm gbh (57%) than <50cm gbh (9%); and (ii) highest for holly, oak and rowan (23-30%), lower for birch and hawthorn (11-13%), and least for alder, ash and hazel (0-3%) (including species with >5 snags). Although 346 live stems ≥5cm gbh died during 1986-98, 210 (61%) collapsed and failed to form snags in 1998. The percentage that did form snags was: (i) higher for stems ≥10cm gbh (40%) than <10cm gbh (25%); and (ii) highest for oak (50%), lower for birch, hazel and holly (32-33%), and least for rowan (19%) (including species with >30

Table 3.6.22: Change in the basal area, density and relative importance of snags in the permanent transects on Clairinsh between 1986 and 1998. Includes all dead standing stems ≥5cm gbh. Relative importance = [% total basal area + % all snags]÷2

	Basal area (m^2 ha^{-1})		Density (n ha^{-1})		Relative importance (%)	
	1986	1998	1986	1998	1986	1998
Oak	0.5	0.5	22	22	27	37
Hazel	0.1	<0.1	67	29	25	12
Birch	0.2	<0.1	37	19	18	12
Ash	0.2	<0.1	5	4	10	2
Rowan	<0.1	<0.1	16	14	6	6
Alder	<0.1	0.1	9	10	4	11
Holly	<0.1	<0.1	10	19	3	7
Hawthorn	<0.1	<0.1	8	2	3	1
Beech	<0.1	-	1	-	2	-
Blackthorn		<0.1	2	14	1	8
Willow	-	<0.1	-	7	-	3
Guelder rose	-	<0.1	-	2	-	1
Bird cherry	-	<0.1	-	1	-	<1
All species	1.1	0.9	177	143	100	100

Table 3.6.23: Fate, throughput and recruitment of snags in the permanent transects on Clairinsh between 1986 and 1998. The table shows the number of snags in each category, including all dead standing stems ≥5cm gbh; (a) includes live stems in 1986 that had died and collapsed by 1998; (b) includes live stems in 1986 that had died and which formed snags in 1998; and (c) includes stems <5cm gbh, <1.3m tall or not present in 1986 and which formed snags in 1998

	Snags in 1986	Fate of 1986 snags by 1998		Throughput 1986-98	Recruitment 1986-98	
		Still standing	Collapsed	(a)	(b)	(c)
Hazel	67	2	65	46	20	7
Birch	37	4	33	32	16	-
Oak	22	5	17	11	17	-
Rowan	16	4	12	41	10	-
Holly	10	3	7	30	15	1
Alder	9	-	9	8	9	1
Hawthorn	8	1	7	8	1	-
Ash	5	-	5	9	3	1
Blackthorn	2	1	1	14	11	2
Beech	1	-	1	-	-	-
Guelder rose	-	-	-	5	2	-
Willow	-	-	-	5	1	6
Broom	-	-	-	1	-	-
Bird cherry	-	-	-	-	1	-
All species	177	20	157	210	106	18

snags). In addition to the 20 snags that remained standing, another 124 recruited during the period. Most of these were small: 75% were <20cm gbh and only three of them were ≥60cm gbh. Most of the throughput and recruitment was of birch, hazel, holly and rowan.

3.6.2.7.2. Dead wood levels, dimensions and condition in 1998

The abundance, dimensions and condition of snags and fallen dead logs/branches was assessed in detail in 1998 (Table 3.6.24). The combined volume and length of these was $19m^3\ ha^{-1}$ and 1384m ha^{-1} respectively, much of which was on the ground.

Most snags were <30cm gbh, <7m tall, had limited decay and/or most bark still present (Table 3.6.24). Much of the snag volume and most of the larger gbh and taller snags were oak. Most logs/branches were also <30cm girth at the point of intersection and had limited decay, but 60% had shed over half their bark. Compared to snags, logs/ branches were generally more decayed and retained less bark: 8 out of 35 logs/branches were rotten or very rotten compared to only 5 out 79 snags ($\chi^2_{(df=1)} = 6.6$, $P<0.05$); and only 14 out of 35 logs/branches retained 50% or more bark compared to out 68 out of 79 snags ($\chi^2_{(df=1)} = 25.5$, $P<0.001$). Oak accounted for 61-71% and birch 14-30% of the total volume/length of logs/branches. Only two oak and one birch log measured 60cm girth or more at the point of intersection. Most oak logs had limited decay, whereas most birch had much decay.

Table 3.6.24: Volume and condition of snags and fallen dead logs/branches as recorded in the permanent transects on Clairinsh in 1998. Cells show the number of snags/logs in each category unless stated otherwise

(a) Snags – based on measurements of snags ≥5cm gbh

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Density (n ha^{-1})	Height			Gbh			Decay state		Remaining bark	
				0-2.5m	3-7m	>7m	5-<30cm	30-<60cm	60-158cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Oak	5.1	104	19	5	9	6	12	4	4	20	-	4	16
Alder	0.7	32	8	2	5	1	3	3	2	6	2	-	8
Blackthorn	0.3	29	7	3	4	-	3	4	-	7	-	-	7
Birch	0.3	61	18	7	10	1	14	4	-	17	1	1	17
Hazel	0.1	18	4	1	3	-	3	1	-	3	1	-	4
Holly	<0.1	27	9	4	5	-	9	-	-	9	-	1	8
Rowan	<0.1	22	7	4	5	-	7	-	-	6	1	2	5
Ash	<0.1	3	2	2	-	-	1	1	-	2	-	-	2
Willow	<0.1	3	2	2	-	-	2	-	-	2	-	2	-
Hawthorn	<0.1	3	1	-	1	-	1	-	-	1	-	-	1
Guelder rose	<0.1	2	1	1	-	-	1	-	-	1	-	1	-
All species	6.6	305	78	31	42	8	56	17	6	74	5	11	68

(b) Fallen logs/branches – based on line transect survey of fallen dead stems ≥15cm girth at point of intersection

	Volume (m^3 ha^{-1})	Length (m ha^{-1})	Girth at point of intersection			Decay state		Remaining bark	
			15-<30cm	30-<60cm	60-110cm	Solid/part-rotten	Rotten/very rotten	<50%	50-100%
Oak	7.4	770	18	5	2	22	3	20	5
Birch	3.7	154	2	2	1	1	4	-	5
Cedar	0.7	62	-	2	-	2	-	-	2
Hawthorn	0.2	31	1	-	-	1	-	-	1
Rowan	<0.1	31	1	-	-	1	-	-	1
Unidentified	0.2	31	1	-	-	-	1	1	-
All species	12.2	1079	23	9	3	27	8	21	14

4. DISCUSSION & SYNTHESIS

4.1. Natural status of the study sites

This first section of the discussion deals with the natural status of the study sites before considering their long-term development. It summarises relevant findings from the study sites and then discusses and compares this material with relevant literature. It considers the effects that past management had on the structure and composition of the stands inherited for study, especially the regeneration that developed after the last major intervention. It also examines the influence of elements that were not present under original-natural conditions.

4.1.1. Inherited structure & species composition

4.1.1.1. Former wood-pasture sites

Three of the study sites (Denny Inclosure, The Mens, Toy's Hill) were traditionally treated as wood-pasture (see Sections 3.1.2.1, 3.2.2.1, 3.3.2.1 for details). These developed into high forest after traditional livestock grazing was abandoned. Beforehand, Denny and The Mens appeared to have been a mosaic of grassland and trees with little scrub, whereas Toy's Hill was more of a heathland. All retained some large, relic wood-pasture trees when they were first recorded. At Denny and The Mens these trees included more oak than beech, some of which were pollards. They were scattered at The Mens and more grouped at Denny. At Toy's Hill they dominated the study area and were mainly large, outgrown beech pollards, with only a few standard oak and beech present.

At Denny and The Mens these old trees were surrounded by a second generation that developed after enclosure. These must have recruited in relatively open conditions and undergone many decades of exclusion. Post-enclosure trees were present in the study area at Toy's Hill, but the area covered was small and such trees were scarce and difficult to

identify, as many had been coppiced or pollarded after enclosure. Most surviving trees in this generation at Denny were beech, though oak persisted well in places. At The Mens, oak outnumbered beech in this generation. There was also a few contemporary ash, birch and/or field maple at one or other of these two sites, suggesting that these and perhaps other light-demanding species (notably hawthorn and hazel) had been more abundant early in the stand development. The evidence from Toy's Hill suggested that beech outnumbered oak in the post-enclosure generation, with many of the beech having regrown strongly after being pollarded or coppiced in the early 20th century. Few other species appeared to form part of this regeneration. However, soil pollen analyses (see Moseley & Moore 1988) showed that birch colonised the site extensively after it was enclosed, before giving way to beech in recent decades. Oak might have been more numerous early on.

Comparable infilling has occurred in other wood-pastures following a decline in traditional grazing/browsing. Between groups of scattered pollards and standards from the original wood-pasture, oak, beech, birch and holly have been the main regenerants in other New Forest wood-pastures, locally supplemented by other species where soil conditions and seed sources permit (Putman *et al.* 1989, Tubbs 2001, Mountford & Peterken 2003). Much the same has happened at Burnham Beeches, Epping Forest and Dendles Wood (Mountford *et al.* 2001b, Rackham 2003, personal observation).

Many factors might have affected the post-enclosure regeneration that developed at the study sites (see e.g. Evans 1988, Harmer & Kerr 1995). It was assumed that most individuals that recruited developed naturally, though some planting might have occurred and some recruits might have been promoted. At The Mens the stands were affected by thinning operations, which must have favoured some individuals. Most certainly it was influenced initially by the stock of seed-producing trees and shrubs present immediately after enclosure. These were generally limited, particularly for certain species. Oak and

beech, two of the main regenerants, were present as seed-bearing trees as was common in traditional wood-pastures (Rackham 2003). Oak would have benefited from dispersal by birds and its ability to grow rapidly in open conditions and to establish in grassland and at the edges of bramble or blackthorn patches (e.g. Bossema 1979, Kollmann & Schill 1996, Löf 2000, Vera 2000, Kuiters & Slim 2003, Bakker *et al.* 2004). Beechnuts are usually less widely dispersed than oak and beech seedlings are less capable of establishing in grassland and grow slowly even when adequately lit. However they tend to be less-preferred by browsing animals, are more tolerant of shading, and often develop as an understorey to other species (e.g. Watt 1923-25, Brown 1953, Newbold & Goldsmith 1981, Putman 1994a, Löf 2000, Gill & Beardall 2001). Although birch was probably scarce as a pre-enclosure tree, this would have presented less of a problem as it regularly produces large amounts of seed that are widely dispersed (see Harding 1981, Atkinson 1992). This also applies, but to a lesser extent, to ash and field maple (see Jones 1944, Wardle 1961, Gordon & Rowe 1982, Kerr 1995). Hawthorn and other shrubs would have benefited from dispersal by birds and mammals (Grime *et al.* 1988).

4.1.1.2. Former coppice sites

The other three study sites (Monks Wood, Langley Wood, Clairinsh) were traditionally treated as coppice-with-standards before being set aside (see Sections 3.4.2.1, 3.5.2.1, 3.6.2.1 for details). Before being set aside to naturally regenerate and develop into high forest, all had most of the underwood cut and many larger trees felled.

When the sites were first recorded, there was a scatter of large individuals present. These represented most (if not all) of the standard trees, singled coppice stools or other individuals that were left uncut at the last felling. Much of the growth present was, however, even-aged regeneration that grew up after the last fellings. This seemed to have generally established without much difficulty unless heavily shaded by retained trees. A

wide range of woody species developed, though the mixture and number of differed according to the soil conditions at and within each site. Light-demanding species were, nevertheless, well represented.

A major part of the regeneration that developed after the last fellings appeared to be from coppice stumps. This was mainly of light-demanding species and species that readily produce stump sprouts (notably ash, field maple, hazel, hawthorn, lime, oak, alder). These had been promoted by: (i) past management (which in some cases had produced large stools of ash, field maple (and particularly) lime and hazel at Langley Wood and Monks Wood that appeared to be several centuries old – see Pigott 1989a, 1991, Peterken 1991, Hæggström 2000, Rackham 2003); (ii) already having pre-formed stool bases and root systems that permitted immediate rapid growth; and (iii) the scale of the last felling which created a high light environment.

Maiden seedlings accounted for most of the other trees that recruited after the last fellings. At Monks Wood these were mainly ash maidens, which appeared to have been promoted by the retention of a few large, seed-producing ash trees. At Langley Wood, ash was evidently scarce in the original coppice underwood and few maidens developed on the drier, apparently less fertile parts of the study transects. However, numerous small, suppressed ash maidens were found on the moderately base-rich stagnogley soils at the start of transect II under a mature birch canopy. It was suggested that these invaded following the death of a large canopy oak around 1960, and there was an ash coppice tree nearby that could have provided a seed source. However, they could have been much older than their size suggested and there was no obvious sign of a gap left by a large oak. At Clairinsh only a few maiden ash developed even where the soils appeared suitable and a large ash tree was present, perhaps because competition from ground vegetation and other woody growth prevented seedlings developing.

Maiden birch developed widely at Monks Wood, though they appeared far less numerous than ash (see also Steele 1973, Welch 1994, Crampton *et al.* 1998) and seemed to have struggled in competition with vigorous coppice growth. Birch maidens were locally abundant on transect I at Langley Wood, but few were successful where lime coppice grew vigorously. They were also less vigorous in the shade of retained oak standards, especially where this combined with vigorous hazel/hawthorn coppice growth. In fact much of the birch woodland in Langley Wood is thought to mark areas where oak was felled long ago, having first weakened the coppice underwood (Peterken 1996). In addition, maiden and coppice birch developed strongly on the damp ground at the start of transect II. They did the same at Clairinsh particularly on the more acidic soils and in larger gaps away from retained trees. At all of these sites, the presence of a few seed-bearing birch and scale of the opening at the last fellings were key factors facilitating birch regeneration (note that although no large birch were found on the transects at Monks Wood, such trees were described as part of the stand mixture in 1914 when the wood was felled progressively – see Steele 1973). Birch is renowned for its early onset of seed production, the regularity with which abundant seed is produced, the distance that it is dispersed by the wind, and its ability to regenerate from seed and grow rapidly when well-lit (Harding 1981, Gordon & Rowe 1982, Evans 1984, Atkinson 1992).

Only at Clairinsh did a reasonable number of oak maidens develop strongly, despite the retention of some large oak trees here and at Langley and a few at Monks Wood. This was partly due to exclusion, but a range of other factors, which are know to affect the establishment and early growth of oaklings, were probably important too (see Watt 1919, Jones 1959, Shaw 1974, Worrel & Nixon 1991, Humphrey & Swaine 1997a, 1997b, Löf 2000, Rackham 2003). In particular, predation by mice and rabbits is known to be an important factor at Monks Wood (Steele & Schofield 1973).

In addition: (i) some field maple maidens recruited at Monks Wood where a few seed-trees were retained; (ii) several lime maidens recruited at Langley Wood, despite lime requiring warm summer temperatures and mature, unshaded boughs to set fertile seed (Pigott 1975, Pigott & Huntley 1981); and (iii) several beech and a few sweet chestnut and sycamore maidens recruited at Langley Wood, which represented expanding populations from nearby planted trees.

Neglected coppice commonly develops as it did at these three study sites, with a scatter of retained standards (mainly of oak) growing amongst dense, mixed-species, coppice regrowth and some maiden recruits often of birch and ash (Rodwell 1991, Peterken 1993a, 1996, Rackham 2003). Many comparable features have, for example, been recorded at Lady Park Wood reserve, which has a similar history of coppice management and final heavy felling before being set aside (Peterken & Jones 1987, 1989).

4.1.2. Comparison with natural woodland

4.1.2.1. Regeneration and initial structure

The main feature of the regeneration observed at the study sites after the last major management intervention was the rapid establishment of a new cohort of trees and shrubs, in which light-demanding species were well represented. This type of regeneration is most usually observed in natural temperate woodland following major windstorm damage where: (i) the canopy is opened widely; (ii) regeneration develops from a range of mechanisms (seed, sprouts, suckers) depending on the species present, the availability and distribution of propagules and suitable micro-sites, and a range of other factors; (iii) fast-growing, light-demanding species are at an advantage; (iv) a minority of overstorey trees/shrubs are usually left standing and some toppled trees survive; and (v) a large volume of dead wood is created along with some upturned root plates and pits (from windthrow) (see Veblen 1992, Everham & Brokaw 1996, Oliver & Larson 1996, Smith *et*

al. 1997, Webb 1999, Franklin *et al.* 2002). Thus, although many of these features were present at the study sites, there would have been little dead wood, no uprooted trees or associated root plate-and-pit formations, and the extent to which sprout-growth dominated the regeneration at the former coppice sites had much to do with the residue of stools developed and left over from past management.

4.1.2.2. Species mixture

The inherited species composition of the study sites bore many similarities to the original-natural mixture of c.6-8000 years ago as postulated from preserved pollen (see Birks *et al.* 1975, Godwin 1975, Greig 1982, Birks 1988, Bennet 1989, Rackham 2003). This was especially the case where the sites had been treated as coppice-with-standards. However, various species appeared to have been reduced or even eliminated, whilst others had increased. At the former wood-pasture sites, there was a distinct lack of lime, elm and (at Denny and Toy's Hill) hazel, whilst beech had become much more prominent. At the former coppice sites, lime was absent and ash, field maple and hawthorn were more prominent at Monks Wood, whilst elm was lacking at Langley Wood and Clairinsh. In addition, some sites had inherited a few non-native trees.

There were various reasons behind the above. The decline of palatable species (especially lime, elm, hazel) was presumably partly connected with grazing/browsing by large herbivores (Turner 1962, Baker *et al.* 1978, Küster 1997, Barker 1998, Tubbs 2001, Rackham 2003). This was most obvious for the wood-pasture sites with their history of traditional grazing, but this applied to the coppice sites as well as parts of Langley had also once treated as wood-pasture, Clairinsh appeared to have once supported a farming community, and many coppice woods were often used for grazing and pannage (Peterken 1993a, Rackham 2003). Other factors that may have been involved in the decline or increase of species are climatic changes (Godwin 1975, Pigott & Huntley 1981), soil

degradation (Dimbleby 1965), Dutch elm disease (Rackham 2003), the introduction, spread and/or promotion of particular woody species by people, and felling of trees (e.g. Cowling *et al.* 2001). Certainly, parts of Monks Wood were cultivated in medieval times, heathland at Toy's Hill would have been managed by burning, all sites had trees cut, beech was favoured at The Mens and Toy's Hill as a fuel for the glass industry in the 16-17th centuries, and Clairinsh and Langley were 'improved' by planting various species.

4.1.2.3. Mammal populations

The abundance and impact of large herbivores in the original-natural woodland of Britain is not well defined (Buckland & Edwards 1984, Vera 2000, Peterken 2001, Bradshaw 2002, Svenning 2002, Bradshaw *et al.* 2003, Kirby 2003, Rackham 2003), which makes it difficult to judge the naturalness of the large herbivore populations maintained at the study sites. Although it is clear that all the sites lacked naturally self-regulating, mixed species, large herbivore populations, free-ranging deer continued to have access and some livestock grazing and pannage was maintained as part of the traditional management at several or perhaps all of the study sites (though this was largely abandoned or discontinued once the sites became minimum-intervention reserves). Particularly significant were the dramatic increases in fallow deer and ponies within Denny Inclosure after about 1960, and in Chinese muntjac deer within Monks Wood from the mid-1980s. In both cases these animals had a major impact on stand development. In addition, all sites except Clairinsh were colonised during the 20th century by American grey squirrels. This had a significant affect on stand development as these small mammals went on to debark trees selectively. In addition, they probably affected regeneration by consuming seeds of certain woody species (see Pigott *et al.* 1991, Rackham 2003).

4.1.3. Conclusions about natural status of study sites

The study sites had clearly been influenced by past management and were not strictly natural (*sensu* Peterken 1996). Some original-natural elements were lacking, whilst other non-native elements were inherited or colonised later. At the time recording started the structure and composition of the stands remained heavily influenced by past management, and also by the conditions and regeneration that developed after the last major intervention. Thus, their initial natural status was not substantially different from other ancient semi-natural woods in Britain treated by low intensity management (Peterken 2000a).

Despite this all the sites inherited or developed various natural features, some of which could be linked to the original-natural woodland of c.6-8000 years ago (others were natural only in a modern context related to their recent treatment by minimum-intervention). Firstly, they were all dominated by original-natural tree and shrub species, with only a few non-native species being recorded (in fact the non-native trees at Clairinsh and Denny were controlled or eliminated). In addition, the species mixture could be broadly described as semi-natural (in modern-day terms) and was not wholly different from that found in the original-natural woodland, though in some cases the predominance of certain species (notably beech) was rather different. Secondly, when the stands under study were initiated after the last major intervention, they were in many ways not unlike natural stands that develop after major wind damage. In fact they all inherited or developed several generations of trees and shrubs, which represented a wide-range of ages and sizes, included at least some large old trees, and created a variety of stand structures (from a relatively simple, two-tiered structure at Monks Wood and Langley Wood to a more complex structure at Clairinsh, Denny and The Mens). These elements are relatively typical of natural temperate stands (Oliver & Larson 1996, Peterken 1996). Thirdly, prolonged treatment by minimum-intervention allowed the sites to naturalise, i.e. operate by natural processes and develop natural features. This generated natural patterns of regeneration,

growth, mortality, damage, canopy gap formation and disturbance (accepting that the stand structure and composition was influenced by past management). Although heavy browsing, as took place at Denny and Monks Wood, has been seen as unnatural, others have suggested that such unrestricted browsing by deer, ponies, cattle and other large herbivores is close to the original-natural regime (Vera 2000). Whatever, the browsing animals at these sites were acting in a natural manner, as were greys squirrels where they occurred, albeit that muntjac deer and grey squirrels are part of the native fauna of other continents, i.e. they can only be considered a modern-natural component.

Thus, the characteristics, developments and processes recorded at the study sites were 'natural' within the modern context of minimum-intervention reserves, but they were only a partial facsimile of the conditions and developments within the original-natural woodland of Britain and were not immune to relatively unnatural influences (e.g. debarking by American grey squirrels).

4.2. Long-term natural development of major species and woodland types

This section deals with a major part of the thesis: the natural development of the study sites after they had been allowed to regenerate following the cessation of traditional management. The first of the following sections summarises the recorded development at each site. This acts as a bridge between the result chapters (Sections 3.1-6) and the subsequent sections that review the performance of each of the major species and long-term development of each of the major woodland types represented.

4.2.1. Summary of species development at each study site

4.2.1.1. Denny Inclosure

When recording started at Denny in the 1950s, oak remained co-dominant with beech in the overstorey. However, although oak was about equally as numerous and fast growing as

beech amongst the oldest generation of overstorey trees, it was less numerous than beech in the middle-size range and rare as a small tree. Moreover, smaller, less vigorous medium-large oak continued to decline in the face of competition with beech, especially before the stands opened after the 1976 drought. Exclusion also left many surviving oak in 1996 with compressed crowns and little sub-canopy foliage (though several near gaps had been part-released and developed new foliage and/or sprouts). Some larger oak died or deteriorated due wind damage (though a few managed to sprout strongly in a pollard-like form), and at least six other large oak that died in the late 1980s and several more that declined unexpectedly appeared to have been debilitated by prolonged drought starting in 1976. This was also suggested by the general reduction in the growth rates of surviving large oak and by the general recovery in these rates during 1988-96 (which corresponded with improved summer rainfall and the release of originally suppressed oak trees).

Beech proved more shade-tolerant than oak. In addition to its dominance amongst subordinate canopy trees in the 1950s, it had also managed to recently recruit many saplings in the understorey, though these were infrequent around the oldest beech trees (but not oak). However, once deer/ponies became numerous after the mid-1960s beech (and other species) stopped recruiting. Even so a good many beech dating from the early 20th century survived in the substratum in 1996, many of which appeared to have benefited from the opening of the canopy (as revealed by their growth rate during 1988-96). Nonetheless, several forms of deterioration set in amongst the older beech and some hitherto vigorous trees died or were left in a poor state by 1996. The oldest, largest beech were badly affected by drought. At least 21 of them died as a result. Some were lost within a few years of the severe drought of 1976. More succumbed by 1988 and a few more died by 1996, all of which had probably been weakened first by the 1976 event. A number of old beech that survived suffered substantial crown die back and/or bark necrosis due to drought. In addition, there was a general reduction in the growth rate of old beech up to

1988, after which they recovered. Secondly, several medium-large beech were uprooted or snapped during windstorms, especially in the windstorms of 1990. In total, wind damage killed 35 overstorey beech compared to only eight oak. In addition, seven beech were uprooted but remained alive on the ground in 1996. The other factor that proved to be a serious problem for beech was grey squirrel debarking. This appeared to have started in the 1970s and worsened during the 1980/90s. It mainly affected beech of 10-40cm dbh, particularly those that had been released into fast-growth. Several were killed completely, whilst others survived but with major die back and/or large wounds.

Thus, despite beech out competing oak and being able to tolerate and regenerate in shade, it was set back by a combination of drought, wind damage, deer/pony browsing and squirrel debarking. During 1959-96 the two species declined similarly in terms of basal area and a slightly higher percentage and number of old oak survived and the same percentage of c.125 year old trees survived (but with beech still outnumbering oak). Only beech survived as 60-70 year old trees.

Holly formed a patchy, but pronounced understorey in the 1950s, which continued to expand to the mid-1960s and particularly in the vicinity of old oak. However, deer/ponies increased and destroyed much of this. Even larger trunks died after being badly debarked. This certainly interfered with the size measurement of holly stems and may have explained the slow-growth of holly during 1964-88. However, the increase in holly growth rates after 1988 correlated with its release from heavy shading.

Few individuals of other species were recorded. Birch and ash both declined due to exclusion, and one of the two surviving yew was in a poor state in 1996. Although sycamore had started to invade in the 1950s, all sycamore saplings were destroyed by

deer/ponies. Indeed, despite the opening of several large gaps after 1976, there was almost no regeneration of any species.

4.2.1.2. The Mens

The main canopy trees present when recording began at The Mens in the mid-1970s were beech and oak. However, more of the oldest individuals were oak whereas most of the younger trees were beech. This trend towards beech dominance continued to 1998 where the stand remained closed or gaps closed in. Oak suffered more from exclusion than beech and the few oak recruits that developed in the gaps created in the 1950/60s were excluded. Nevertheless, oak proved relatively competitive and continued to outnumber beech amongst the largest overstorey trees. Several oak suffered from wind damage, particularly in the 1987 windstorm (but also through to 1998). Most suffered trunk/crown-snapping rather than uprooting. Although less oak were wind-damaged than beech, most were large trees and the basal area lost was somewhat greater. A third of the oak badly damaged in 1987 survived in 1996. These were mainly trunk/crown-snapped tree that were sprouting strongly higher up. Few uprooted oak survived. Surviving oak bordering larger canopy gaps had generally expanded into these by 1998, often from epicormic trunk/crown sprout growth. No effective oak regeneration was recorded in the 1987 windstorm gaps.

Although beech suffered less from exclusion than oak and remained fairly numerous as a moderately fast growing substratum tree, it nonetheless remained strongly suppressed where it grew below canopy beech and hardly managed to recruit where the stands remained closed. It also had several small-medium substratum trees damaged and many overstorey trees uprooted or broken in the 1987 windstorm. Of the trees that were directly damaged by the storm, relatively more were uprooted than oak, indicating that beech was less firmly rooted. 40% of beech badly damaged in the 1987 storm survived in 1998, with the same percentage surviving trunk/crown-snapping as survived uprooting. In addition,

many beech bordering gaps created in the 1987 storm had been were released and expand into the gaps though a combination of crown, high sprout and low lateral branch growth. However, recovering, released and especially pole beech became the focus of grey squirrel debarking (which appeared to have been limited beforehand). By 1998 a third of beech sized 60-120cm had been severely stripped or ringed, with some similar sized beech having been killed completely. Beech managed to regenerate in several of the 1987 windstorm gaps, though the number of established seedlings/recruits was relatively limited, patchy and generally beech recruits were slow growing.

Ash, birch, cherry, field maple and wild service also appeared capable of developing into canopy trees. However, these struggled to maintain a place in closed stands, though the last two species did prove reasonably shade-tolerant. Nonetheless, ash and birch did manage to recruit some vigorous saplings in the centre of one of the larger gaps created by the 1987 storm. In addition, a single vigorous wild service sapling grew up in a windstorm gap.

The most numerous understorey shrub recorded was holly. It developed despite being over-topped, slow growing and suffering some damage from falling trees/branches. Moreover, it recruited strongly in places. This appeared to have started in the gaps opened in the 1950/60s and was facilitated strongly where the canopy was broken by the 1987 windstorm. Hawthorn and hazel behaved similarly to holly, but they were less numerous and proved more light demanding. Six minor understorey species were recorded. Elder, goat willow, broom and gorse proved strongly light demanding and were restricted to canopy gaps. Yew and crab apple proved more shade-tolerant (especially yew) and both developed vigorously when released in gaps.

4.2.1.3. Toy's Hill

The records from Toy's Hill showed that beech was the dominant canopy tree here before the 1987 storm struck. Many beech trees were in fact multi-stemmed, outgrown pollards that had regrown strongly after cropping early in the century. Some of the bollings on these were exceptionally large and perhaps two-three centuries old. In addition, several coppice and maiden beech were present, mainly as subordinate trees. Most large canopy beech were uprooted or snapped off in the 1987 storm, and most understorey beech were hit and left broken or crushed. The few remaining standing beech also lost limbs. By 1998, many of the larger toppled or snapped beech had died. Some of the survivors, however, showed some signs of recovery, though these had become the focus of grey squirrel debarking. Survival of smaller wind-damaged beech was generally higher than for large trees with about half having started to redevelop from basal or trunk sprouts. Very little new beech regeneration developed after the storm.

Few oak were present before the 1987 storm struck. No doubt any oak that had been present beforehand had struggled to compete with beech. Two of the three oak recorded in the study plot were brought down in the 1987 storm, and the remaining standing tree had part of the crown blown out. By 1998, however, the standing oak was shooting well and one of fallen trees had developed several strong sprouts near the base. Other oak regeneration remained very limited.

Although birch was absent from the study plot before the 1987 storm struck, it regenerated strongly in many places afterwards and by 1998 formed dense thickets within which the weakest saplings had already been killed or become suppressed. Other species were scarce before the 1987 storm. The understorey contained only a scatter of shade-tolerant holly bushes and a single rowan individual. Although these were damaged in the 1987 storm,

they all regrew strongly, along with some other holly individuals and a single rowan sapling.

4.2.1.4. Monks Wood

Ash had become the dominant overstorey tree when recording started at Monks Wood in 1985. It had generally grown taller and faster than other species and continued to do so through 1996. In addition, it also persisted fairly well in the substratum. Many ash individuals were from coppice, but in places ash maidens remained prominent. Although ash remained vigorous, a few larger stems had collapsed or been broken over 1985-96 (probably during windstorms), many of which had been growing on a lean and/or were poorly attached.

Field maple remained widespread, though it was less numerous and generally slower growing, less tall and subordinate to ash. However, it proved rather tolerant to overtopping by ash. Several of largest field maple trees died during 1985-96, some of which were windblown. Others, however, died standing and it seemed like they might have been weakened by drought in preceding years.

Hawthorn and hazel developed widely, but had soon become overtopped by ash and (in places) field maple and oak. Nonetheless, both proved relatively tolerant of overtopping and, despite suffering from exclusion, remained surprisingly abundant throughout 1985-96. Hawthorn was more numerous than hazel, partly because hazel showed clear signs of decline across the population size-range before and during 1985-96. This was partly due to exclusion, but some hazel stems were struck or collapsed, muntjac deer ate down many basal sprouts and probably killed other small hazel stems, and several large stems and old stool bases that died, deteriorated or had noticeable decay appeared to be suffering from some additional factors, perhaps senescence combined with drought and fungal attack.

Nevertheless, hazel proved quite capable of developing erect, vigorous replacement stems from basal or trunk sprouts.

Oak persisted mainly as a canopy tree from standards retained at the last felling. It proved rather intolerant to overtopping and many oak recruits appeared to have been excluded. However, at least some survivors appeared to be post-1920 recruits that had grown strongly (it would be useful to take cores from these to determine their age). Many surviving oak were still in a dominant position, but others were slow growing and appeared to be losing growing space to ash.

Some other light-demanding trees had obviously regenerated strongly after the c.1920 felling, but had suffered from exclusion and become scarce by 1985/96. Very few birch survived to 1996, partly because numerous large birch across the wood were killed by severe drought in 1976. Even so, this certainly accelerated mortality that would have been expected to arise anyway through exclusion (see also Peterken 1994). Indeed, many birch were excluded during 1985-96 and the survivors were struggling in competition with ash. Aspen and goat willow had probably been locally abundant in the early stand, but the last few aspen recorded on the study transects in 1985 were dead by 1996, whilst goat willow persisted in only three places predominately on wetter ground and close to rides. Other records from the wood reveal general declines in birch, aspen and willow (Steele 1973, Welch 1994, Crampton *et al.* 1998).

Several other minor species were recorded. These included wild service and crab apple, which had probably always been scarce. Both proved to be slow growing, but relatively shade-tolerant. Of the six minor shrubs species recorded in 1985, blackthorn, privet and dogwood were locally numerous. These had benefited from side-light from rides, especially blackthorn that had proliferated at the end of one of the transects. Few elder,

guelder rose and spindle bushes were present in 1985, though they were probably more numerous early on. All of these species suffered moderate or high mortality during 1985-96. Although exclusion was involved, muntjac deer were also a factor. This was clear enough for privet (which had many bushes reduced to low live growth), and was strongly implicated for spindle and dogwood that had many surviving stems debarked by deer. Studies elsewhere in the wood have shown that muntjac readily browse coppice regrowth of dogwood, privet and other species (Cooke 1994, Cooke & Farrell 2001).

Muntjac deer appeared to have also destroyed other low woody growth. Although regeneration appeared to have been strongly suppressed after the stands closed in about 1930, some fresh regeneration was evident in 1985. This included many ash seedlings, which had become locally abundant where birch had been lost, on the margins of rides, and/or where the understorey had part-collapsed. Many of these were short seedlings, but some had grown to or over 1.3m tall and looked capable of developing further. In addition, some seedlings/suckers/saplings of various other species and a substantial portion of the small stems on hazel bushes looked to have established recently. Unfortunately, much of this regeneration was destroyed during 1985-96, the most obvious culprit being muntjac deer, which appeared to have also eaten out most of the bramble growth present in 1985.

4.2.1.5. Langley Wood

Small-leaved lime was one of the main species at Langley when recording started in 1986. It had developed strongly in places along transect I mainly from groups of coppice stools. These had excluded all other nearby post-1940 recruits, save for the very fastest grown birch and any retained oak standards. Each cluster of stools produced numerous persistent stems, though only the most dominant developed into tall, straight poles and maintained a high increment rate. A scatter of lime maidens managed to recruit nearby at a distance of c.5-20m. Although these were overtopped in 1996, they remained reasonably healthy and a

few were making headway into the sub-canopy, particularly below birch or where oak standards had lost boughs.

Dominant birch trees had also grown rapidly, particularly on transect I and on the damp ground at the start of transect II. However, even these struggled whenever they were in direct competition and shaded by lime or oak. Nevertheless, a surprising number of birch survived where overtopped by other birch. Although the fastest birch had grown rapidly, several medium-large trees had or appeared to be have gone into decline after a few decades of growth. These included several birch snags and toppled trees recorded in 1986 and several more that were uprooted or wind-broken during 1986-96 (possibly these had been weakened or killed beforehand by the severe drought of 1976). In addition, some of the largest birch that survived grew only slowly over 1986-96, and although the largest-crowned canopy birch appeared healthy enough in 1996, others were struggling to maintain their place.

Few ash managed to develop into canopy trees within the drier parts of the study transects. However, some suppressed ash saplings were recorded here in 1986, a few of these were released below gaps and developed strongly upwards by 1996, and a scatter of new ash seedlings established. Similar changes took place amongst the mass of ash saplings on the stagnogley soils at the start of transect II, with a few being released following the windthrow of birch and die back of oak in this area. It appeared that ash would in time probably end up replacing birch here, as well as developing on drier soils elsewhere.

The oak standards retained at the last felling persisted well with many remaining in the canopy and still growing well in 1996 (particularly in terms of their basal area increment). However, oak proved remarkably intolerant of overtopping. It might also have suffered from drought or another factor as some trees died standing during 1986-96 and left canopy

gaps. Certainly several trees had branches torn out by windstorms and some weakened trees might have been windthrown. It seemed that very few oak recruited after the last felling: those that did had mostly been excluded or were struggling in 1996. Nevertheless, at least a few seemed to have grown into reasonably strongly canopy trees (these could be usefully cored to check their age).

Hazel remained common as a multi-stemmed, understorey bush on parts of transect I and much of transect II. It appeared to have suffered greatly where overtopped by lime. However, it remained rather abundant where it grew between a scatter of widely spaced oak standards and occasional birch. It also responded well to the partial opening of the canopy before and during 1986-96, producing many new stems on existing stools and having some new individuals and numerous seedlings establish. It was notable how infrequent large hazel stems were, that mortality of these was fairly high, and that these tended to be growing on a lean and non-vigorously. This left room for recruiting stems to grow straight up into the space vacated by larger leaning stems, in a form self-coppicing.

Hawthorn was similar in many respects to hazel, but was far less common and often individuals had been reduced to one or a few main stems. It also responded to the increase in canopy gaps over 1986-96, with a large number of new seedlings and individuals establishing and several new vigorous trunk shoots developing.

Other species were or had become scarce by 1986/96. Notable were several beech had developed into strong medium-sized, sub-canopy trees, but which by 1996 had been badly debarked by grey squirrels, as had most of the sycamore. Four sweet chestnut survived and the largest had grown vigorously. Only a small number of field maple, crab apple, yew, alder, and goat willow survived, many of which were overtopped and suppressed.

Blackthorn and holly were scarce, but during 1986-96 had numerous suckers/seedlings establish, as did a few short hornbeam seedlings.

4.2.1.6. Clairinsh

Oak was one of the main species recorded at Clairinsh over 1961-98. It became increasingly dominant in the core, base-rich marginal and base-poor marginal woodland. It was also recorded as a minor species in the shoreline woodland. The oak population ranged from medium-large trees to smaller, post-1913, seedling and coppice recruits. Most of the latter failed to grow into the upper canopy and had been excluded by 1998 having suffered from competition from larger neighbouring oak and other tall trees. Nonetheless, a surprising number persisted in the substratum. Most of older oak remained firmly placed in the canopy and grew reasonably well over 1961-98. However, many suffered some form of wind damage during the severe windstorm of 1968 or in later gales. Several trees were uprooted, snapped or lost major parts of their crowns, with about one in five surviving trees in 1998 having sustained notable wind damage. Only one of six oak trees uprooted in 1968 managed to survive to 1998, but some that were snapped managed to expand and/or resprout strongly, and several undamaged trees were released into gaps.

Birch was an important species in the core and base-poor marginal woodland, but was only occasional or scarce in the base-rich marginal and shoreline woodland. It regenerated well in gaps within the core and base-poor marginal woodland in the early 20th century. However, it proved rather intolerant to overtopping and declined as regeneration groups filled and the canopy of retained oak expanded. A few large birch were also lost during windstorms. Nonetheless, a scatter of retained birch and a moderate number of birch recruits grew into and sustained themselves as relatively fast-growing canopy trees. In addition, a surprising number of birch survived as suppressed stems in the substratum, a

few of which had been released below gaps. A very few birch managed to recruit in gaps created by the 1968 windstorm.

Ash was recorded as only a minor species in the core and base-poor marginal woodland, no doubt because the soil conditions were limiting for ash growth. It was present in the base-rich marginal woodland, but in the taller part of this stand (where large oak predominated) it suffered from exclusion and the only large ash present was toppled in the 1968 windstorm. Even so, a few younger ash between the oak managed to develop into the canopy. Within the remainder of this stand and on the adjoining higher ground of the shoreline shingle woodland (where the stands were rather low), ash remained important and grew mainly as multi-stemmed coppice individuals. However, it was only a minor species close to the island edge.

Alder was important in only two woodland areas recorded at Clairinsh. In the base-poor marginal woodland several alder were recorded in the canopy in 1961. However, most of these had been excluded or become strongly compressed and very slow growing by 1998. Alder was also prominent close to the shoreline at the north end of the island, though it lost out to competition from birch and ash by 1998.

Holly was one of main understorey species recorded. It occurred primarily in the core and base-poor marginal woodland and proved to be very shade-tolerant. In addition to a few old tree-like holly, many smaller holly individuals established. The latter appeared to have started to develop from the about 1950s, as low, layering growth around larger bushes or more widely dispersed seedlings. Holly continued to develop strongly through to 1998. Although a few holly stems died after being struck by falling trees/branches, others recovered from such damage and some showed obvious signs of release below gaps.

Rowan also developed strongly in the understorey. However, it grew more as a small-medium tree and extended into the base-rich marginal and higher ground of the shoreline shingle woodland. Many larger rowan were multi-stemmed and probably developed after being coppiced in the early 20th century. Along with these, numerous small rowan had seeded in by 1961, with more doing the same during 1961-98. A few larger and several smaller rowan were crushed by falling windblown trees. Some of these died or were left slow growing. Nonetheless, canopy gaps created by wind damage did release several well-established rowan.

Hazel was present as a component of the understorey in the core and base-poor marginal woodland in 1961. Most hazel appeared to have been coppiced in 1913 and developed well initially. However, by 1961 they had become overtopped and some large individuals below oak had gone into severe decline. Nevertheless, some small hazel individuals and stems may have still recruited recently. Hazel declined strongly after 1961 mainly due to exclusion, though some stems were broken by windstorm debris. By 1998, however, the population showed signs of recovery below the now broken canopy. Several individuals had developed vigorous basal/trunk shoots and a few new seedlings and layers had recruited. It also formed part of the understorey in the base-rich marginal woodland where the canopy remained more open. In fact, during 1961-98 it developed further and formed some exceptionally large stools.

A range of minor species was also recorded. Most notable were hawthorn, blackthorn and guelder rose. These persisted primarily as part of the mixed understorey in the open parts of the base-rich marginal woodland and on higher ground of the shoreline shingle woodland. In addition, grey willow formed a thicket of multi-stemmed growth on the ground adjoining the loch edge. This developed strongly during 1961-98, particularly because several individuals collapsed and rooted into washed-up shingle. A few beech,

larch, Scots pine and western red cedar grew vigorously, but most of these were cut out as non-native species. Nevertheless, two beech saplings grew on vigorously and by 1998 were joined by a few more beech saplings.

4.2.2. Synthesis and comparison of natural development of major species

In the following sections the key features of natural development are indemnified for each of the major species recorded across the study sites. This material is compared to relevant literature and a general profile of the ecology of each species in natural stands is outlined. Details of the performance of the species at a particular study site are given in the site result sections (Sections 3.1-6) and site summaries (Section 4.2.1.1-6).

4.2.2.1. Beech

The records of natural change in beech on acidic-mesotrophic brown earth and stagnogley soils, as recorded at Denny, The Mens, Toy's Hill and (to a lesser extent) Langley Wood and Clairinsh, emphasised its: (i) regenerative capabilities from seed within relatively shady, closed stands and in small-medium gaps; (ii) tendency to establish patchily and grow slowly; and (iii) ability to persist in the substratum, develop into a tall, long-lived, dominant tree, and compete vigorously with and/or replace oak, ash, birch and other species in closed stands.

These aspects are widely appreciated. Beech seedlings are normally slow growing, seed production/establishment is notoriously erratic, seed predation is often severe, and seed dispersal limited. Beech seedlings are, however, tolerant of heavy shade, generally less preferred by deer than other broadleaves, and can form as advance regeneration below closed stands and develop upwards below part-broken canopies. Beech normally grows relatively slowly, but maintains a steady growth-rate for many years. It tends to develop best on deep, mesotrophic soils, but and struggles on extremely dry and waterlogged soils.

It avoids exclusion because of its shade-tolerance, and often retains a relatively deep, multi-layered crown and eventually reaches 25-30m in height. In mixed stands beech tends to replace faster-growing but shorter-lived, light-demanding trees, particularly ash and birch (Watt 1923-25, 1934, Tansley 1939, Bourne 1942, 1945, Brown 1953, Ashby 1959, 1967, Jones 1952, Hamilton & Christie 1971, Penistan 1974, Bossema 1979, Aldhous 1981, Newbold & Goldsmith 1981, Gordon & Rowe 1982, Evans 1984, 1988, Linnard 1987, Gurnell 1993, Grime *et al.* 1988, Rodwell 1991, Savill 1991, Harmer 1994, 1995, Putman 1994a, Harmer & Kerr 1995, Pakenham 1996, Hilton & Packham 1997, Packham & Hilton 2002, Mountford 2003, Rackham 2003).

Although beech was shown to have a strong capacity to regenerate from seed, it was nonetheless hindered by various factors. The inability of beech to regenerate beneath its own canopy at Denny and apparent lack of beech advance regeneration at Toy's Hill, may have been connected with the build up of more acidic conditions and particularly mor humus beneath its own canopy, which is considered inhospitable to the establishment of beech (Watt 1923, Harley 1939, 1949, Brown 1953, 1960, Dimbleby & Gill 1955, Pigott 1989b, Evans 1988). The records from The Mens showed that regeneration of beech developed most strongly in small-medium gaps and below part-broken canopies where light levels were at least moderately increased. Despite its shade-tolerance and ability to grow well as a sub-canopy to ash or birch (e.g. Peterken & Jones 1987, 1989, Emborg *et al.* 1996, 2002), it is known that height growth of beech seedlings declines rapidly below about 20% of full sunlight and branches become distinctly flattened and, although moderate shading can stimulate height increment of beech seedlings, dry weight and diameter increment are greatest in lightly shaded conditions. In addition, heavy shading causes poor root growth, reduced absorption of nitrogen, and makes individuals more prone to drought and other debilitating factors (Watt 1923-25, Harley 1939, Brown 1951, 1953, 1955, Dowell 1956, Van Hees 1997, Collet *et al.* 2001).

Seed production and dispersal may have affected recent beech regeneration at the study sites. The records from Toy's Hill indicated that few beech seedlings ever established after the 1987 storm, perhaps because little seed was produced (or seed predation was high), but more obvious was the scarcity of seed-producing beech within the stand after the storm. In larger windstorm gaps at The Mens, poor dispersal of seed into gap centres appeared to have limited beech regeneration. Similarly, very little beech regeneration developed in other heavily damaged beech stands on acidic clay and rendzina soils at Shellem Wood, Noar Hill Hanger and Ashford Hanger after the 1987 storm (Mountford 2002a, Mountford 2004, Mountford & Ball 2004). As beech regenerates mainly close to fruiting trees (as beechnuts fall straight down and are not blown or dispersed far by seed caching animals), gaps in mesotrophic beechwoods are characteristically filled with only a fringe of slow growing saplings around a core of birch and/or ash (Watt 1923-25, Brown 1953, Jensen 1985, Janßen 2000, Mountford & Savill 2004).

Deer also played a part in hindering beech regeneration. Although beech is not an especially palatable tree (Peterken & Jones 1989, Gill & Beardall 2001, Harmer *et al.* 2001), some seedlings at Toy's Hill and The Mens suffered from deer browsing, perhaps because roe deer were present which find beech palatable (Brown 1953, Gill 1992). In addition, beech stopped regenerating at Denny because of browsing/grazing by deer and ponies, which was particularly severe. The latter forms part of a recent widespread failure of tree regeneration across the New Forest, due to an upsurge in large herbivores (Putman *et al.* 1989, Tubbs 2001). At Dendles Wood reserve, a combination of fallow and roe deer and occasional trespass by sheep and cattle has been sufficient to arrest beech regeneration (Mountford *et al.* 2001b). Expected regeneration of beech has also been prevented at Lady Park Wood reserve due to an upsurge in fallow deer (Peterken & Mountford 2002). Although beech seedlings can be protected from large herbivores by the cover afforded by fallen trees, coarse ground vegetation, and prickly plants (Watt 1925, Morgan 1987a

1987b, 1991, Sanderson 1996, Vera 2000), this was not the case in Denny Inclosure nor the unenclosed part of Denny (Mountford & Peterken 2003), where holly and bramble were largely destroyed and no tree regeneration developed in the face of high herbivore pressure. Given the shade-tolerance of beech and its low palatability, it may well develop with some protection if fewer herbivores are present following the model described by Morgan (1987b). This is also suggested by evidence from the windstorm gaps recorded at The Mens, where deer were relatively scarce and the (less heavily shaded) margins of holly bushes provided protection for beech seedlings against browsing.

The final main factor hindering beech regeneration at the study sites was competition from other vegetation. This may well have been inhibited beech regeneration at Denny, as many of the gaps had filled with the coarse grassy vegetation. At The Mens, dense holly growth partly checked the development of some beech seedlings, though some still looked like they would grow up through this. Beech seedlings are slow growing and vulnerable to root competition and overtopping, especially during the early years of establishment. They often become swamped where coarse ground vegetation develops, especially bramble, bracken and/or coarse grasses. Nevertheless, given time they can grow up through bramble, especially on the edge of canopy gaps (Watt 1923-25, Jones 1952, Brown 1953, 1957, Evans 1984, 1988, Peterken & Jones 1987, Mountford & Savill 2004).

The records from this study also emphasised that beech is vulnerable to: (i) grey squirrel debarking as a fast-growing, pole-sized tree; (ii) drought as a large tree; and (iii) wind damage as a large tree (and also indirectly as substratum tree). However, they also showed that beech could make a recovery after being damaged and benefit from release.

Grey squirrel debarking was found to be a particularly important factor. This is a recent phenomenon that has become widespread in woodland across southern England.

Particularly vulnerable are fast-growing, 10-40cm dbh, beech poles that have a high phloem (sap) content, and which are located in stands that have been recently opened, where there is a history of debarking, a high density of squirrels, a major component of beech, and a diversity of seeding tree species (Kenward 1982, 1983, Rowe 1984, Rowe & Gill 1985, Kenward & Parish 1986, Kenward *et al.* 1988a, 1988b, 1992, 1996, Mountford 1997, 2003, Mountford & Peterken 1999, Mountford *et al.* 2001b, Mountford & Peterken 2003, Rayden & Savill 2004). Squirrel debarking has become so severe that it is widely regarded as the single most serious limitation to the development of pole beech into mature trees. This is evident particularly in opened stands, where pole beech have been released into vigorous growth, as in The Mens and Denny Inclosure. Even if pole-sized beech are kept slow growing in closed stands the most vigorous are still typically severely debarked (Mountford 2003). Although larger beech rarely suffer severe trunk debarking, they are nevertheless frequently debarked along their crown branches (which then tend to snap during windstorms) and also around their bases. This was certainly the case at The Mens, Denny and Toy's Hill where several larger beech lost branches following squirrel debarking. Given the increased incidence of branch- and trunk-snap in debarked trees and vulnerability of beech to fungal attack where the bark is wounded (Cartwright & Findlay 1946), it seems unlikely that pole beech will grow into replacement canopy trees and neither these nor larger beech will live as long as their predecessors. Attempts to limit squirrels populations and the damage they cause have proved equivocal (see Rayden & Savill 2004). At Langley Wood about 300 squirrels were culled in 1995, but this did little to stop debarking to beech.

Drought proved to be a major limiting factor for mature beech (unlike most other species), at least at the study site at Denny. The deterioration recorded here following the 1976 drought was in fact repeated elsewhere in mature beechwoods across southern England, from East Anglia to the Welsh borders (e.g. Lonsdale 1980, Lonsdale *et al.* 1989, Rackham

2003, Mountford 2004). Across the New Forest an estimated 4500 beeches were killed (Tubbs 2001). Its effects were apparently exacerbated by the shallow-rooting capacity and water demands of mature beech. Although it impacted strongly on beech on shallow, free-draining soil it also had a major impact on stagnogley soils (as found Denny), as such soils waterlog in winter and restrict the depth to which beech can root (Power 1994). It was notable that beech did not suffer greatly at The Mens, where the soils are deeper and more freely draining. Although no drought impact was recorded at Toy's Hill, trees here probably suffered as the soils are rather shallow and free-draining. The same patterns of crown die back and bark necrosis in mature beech, immediate mortality and slow terminal decline, death of small beech groups, and reduced-growth in surviving trees recorded at Denny was repeated at Lady Park Wood reserve (Peterken & Mountford 1996). The delayed mortality was often associated with disorders to which mature beech are normally resistant: many trees that died or were severely stressed developed strip cankers within a year or two where previously dormant fungal species spread into the sapwood (Chapela & Boddy 1988, Hendry *et al.* 2002); *Nectria coccinea*, a normally weakly pathogenic fungi involved with beech bark disease, caused severe bark necrosis in some old trees (e.g. Lonsdale 1980); at Denny, spreading rhizomorphs of honey-fungus attacked and killed weakened beech (Manners & Edwards 1986); Day (1946) considered drought to be one of the prime factors in the dying of roots on mature beech on calcareous soils overlying chalk and the consequent development of butt-staining/rot from *Ustulina vulgaris* fungi. Less severe droughts in 1983-84 and 1989-90 produced only moderate crown deterioration in beech (e.g. Lonsdale 1985, 1986, Innes 1992).

In addition to drought, mature beech also proved vulnerable to wind damage. This was particularly apparent from Toy's Hill study site, where beech was windthrown on a remarkable scale. This appeared to be due to a combination of factors (Whitbread 1988, 1991, Peterken 1996). The site was apparently struck by some of the severest gusts

generated by the 1987 windstorm and lay exposed on the highest plateau in Kent. The beech growing here were outgrown pollards, with several large, long secondary trunks attached to each bolling. These were evidently firmly attached to the bolling top (it was surprising that more did not simply snap off), and acted like long levers on the short bollings enough to cause the whole tree to uproot (smaller beech pollards generally suffered more from snapping than uprooting, presumably because the secondary trunks on these were shorter and less well attached). Moreover, the beech here were only superficially rooted in shallow soils, as indicated by the dimensions and prominence of hinged root plates (Allen 1992). In addition, the view was that the 1987 windstorm was especially damaging because the trees were still in leaf and the soils had been saturated by heavy rainfall beforehand (Whitbread 1991).

Beech did not suffer such extreme wind damage at the two other study sites where it was abundant, i.e. The Mens and Denny. Nevertheless, a number of mature beech trees were also brought at these sites, mainly in the 1987 (The Mens) or 1990 (Denny) events, and again with relatively more trees being uprooted than snapped. Beech was in fact widely damaged across south-east England in the 1987 windstorm. It suffered particularly on shallow chalky soils, stagnogleys, and sands and gravels, which permitted only shallow or infirm rooting, and also on exposed slopes and plateaus where many mature, shallow-rooted beech were toppled. As found in this study, it suffered moreover from uprooting and tilting with decrowning and trunk breakage being only about half as frequent (Whitbread 1988, 1991, Grayson 1989, Cutler *et al.* 1990, Peterken 1996, Mountford 2004, Mountford & Ball 2004). Nevertheless, sporadic severe gusts to best explain the scattered pattern of gaps that was created in The Mens study area. In a detailed study of the impact of a major windstorm in 1999 at Suserup Skov and Draved Skov reserves (Denmark) (Bigler 2002a, 2002b, Emborg *et al.* 2002, Wolf & Bradshaw 2002, Wolf *et al.* 2004), beech also proved more susceptible to uprooting than trunk/crown-snapping. Mature beech have suffered

from uprooting during windstorms in recent decades at other minimum-intervention reserves, including Fontainebleau in northern France (Koop & Hilgen 1987, Pontailler *et al.* 1997, Wijdeven 2003a) and Zoniënwoud in Belgium (De Keersmaeker *et al.* 2002). Many decay fungi affect the aerial parts or roots of beech and render them liable to wind damage, including *Formes formentarius,* various species of *Ganoderma, Pleurotus ostreantus, Meripilus giganteus* and *Ustulina deusta* (Brown 1953, Lonsdale 1985, 1986, personal observation).

Not all the beech at the study sites that were damaged by windstorms or drought ended up dying. Several not only survived, but also showed signs of making a significant recovery after being uprooted, broken or suffering crown die back. These included several large uprooted trees at Denny, The Mens and Toy's Hill that remained alive on the ground and in reasonable condition, as has happened at Dendles Wood reserve (Mountford *et al.* 2001b). In some cases such toppled trees have produced vigorous new shoots on the trunk or branches (but not at the base), though it was unclear if these would survive long as they had become the focus of grey squirrel debarking. Rackham (2003) also studied the survival of beech uprooted in 1987 storm and found this to be as high as 86% after 10-15 years. This compared to 40% survival recorded at The Mens and only 15% at Toy's Hill. Mountford (2004) and Mountford & Ball (2004) also found survival of uprooted beech was poor at Noar Hill and Ashford Hangers reserves. The most obvious cause was drought, as these three sites all had thin, dry soils and many trees were left largely detached from their original root systems. Rackham (2003) also noted that the dry summers of 1989, 1990 and 1995 killed off uprooted trees, though shade was more influential such that more uprooted oak and sweet chestnut died than beech.

Many other (mainly part-broken) beech at Denny, The Mens and Toy's Hill study sites made some form of recovery following drought or wind damage. On some trees the growth

that developed was notably vigorous, as it was on many undamaged beech that were released where the canopy was broken and particularly around and below larger gaps. This was achieved through a combination of crown expansion, epicormic sprout growth on the upper trunk/crown branches, and (on smaller trees) basal sprout growth. Unfortunately, grey squirrel debarking subsequently killed some branches and sprouts that developed. Comparable patterns of response have been recorded on beech at other reserves (e.g. Mountford *et al.* 2001b, Mountford & Ball 2004) and can be observed widely. It was also apparent from the outgrown pollards at Denny, The Mens and Toy's Hill, that beech can develop into large trees after this type of damage. This was despite it having a reputation to respond poorly to pollarding and coppicing, though this poor response seems to be associated with large, neglected trees and especially where all the crown branches are removed simultaneously (Mitchell 1989, Dagley & Burman 1996). This conclusion was generally supported by the response of large damaged beech recorded at the study sites. In particular, it was notable how several surviving standing pollards at Toy's Hill that retained a few surviving large secondary trunks produced vigorous sprouts from or near to the bolling top, and how large beech bordering gaps at The Mens made notable growth from low lateral branches and epicormic sprouts. Beech typically retains or develops a sheath of low branches/ epicormic sprouts in closed stands (Nicolini *et al.* 2001), which evidently give it an advantage in recovering from damage and when filling canopy gaps or developing when released from suppression. Beech generally responds well to release after many years of suppression, though excessive opening of mature stands over 100 years old can lead to 'sun scorch' on the remaining trees and result in stand collapse (Evans 1984). Koop (1987) reports that beech is capable of layering where branches or fallen trunks come into contact with the ground surface. However, such an event was observed only once across all the study sites.

Some of the beech recorded at Toy's Hill, Denny and The Mens study sites were approaching the maximum age and size expected for beech. These were probably at least 300 and possibly 400 years old, and included trees up to 380, 486 and 570cm gbh, all of which were outgrown pollards. Ancient beech trees are relatively rare in England. Typically they are aged 300-400 years and often have been pollarded and are growing on infertile soils (Tubbs 2001, Rackham 2003). Some mature beech at the study sites had already been killed by drought or windstorms or survived with poor crowns. Most others lacked the spiky crown appearance associated with vigorous growth. Nevertheless, others appeared healthy enough, most were still growing well in terms of their basal area increment, and there were few signs that old beech had succumbed simply to old age.

4.2.2.2. Oak

Records were available from all six study sites on the natural development of oak in various stand mixtures and on a range of soils types, including calcareous, mesotrophic and acidic brown earth, stagnogley and gley soils.

Firstly, these emphasised that oak can grow into and persist as a tall dominant tree. However, many oak trees proved intolerant to overtopping, and the degree to which it predominated depended greatly on the extent to which it faced direct competition with other tree species. Only where it was firmly established in the canopy did it prove competitive with beech at Denny and The Mens, with ash at Monks Wood, with small-leaved lime at Langley Wood, and with birch at Clairinsh. In tended to persist better in the substratum at Clairinsh only where it was overtopped by light crowned birch and represented mainly by sessile oak, which is more shade-tolerance than pedunculate oak (Jones 1959, Jarvis 1963, 1964, Shaw 1968a).

Oak is widely recognised as being a shade-intolerant tree that tends to suffer from exclusion in direct competition with other trees. This is exacerbated by its relatively slow rate of growth. However, if sufficiently well lit, it can maintain a moderate rate of growth longer than most other broadleaves, and commonly makes 25-30m in height across a range of soils including: (i) mesotrophic soils (but it struggles to compete with beech or ash if these are present); (ii) more acidic soils (where it is more or less equally matched with beech); and (iii) more strongly acidic soils and transitions to gley soils (where it can outstrip beech) (Watt 1923-25, 1934, Tansley 1939, Brown 1953, Jones 1959, Hamilton & Christie 1971, Newbold & Goldsmith 1981, Evans 1984, Peterken & Jones 1987, 1989, Grime *et al.* 1988, Rodwell 1991, Savill 1991, Peterken & Jones 1987, 1989, Peterken 1993a, Mountford 1994, Mountford *et al.* 2001b, Rackham 2003).

The records also showed that oak largely failed to regenerate or even produce many well-established seedlings across the study sites (at least in recent times). Oak also regenerated rather poorly from seed in other woods damaged by the 1987 windstorm (Mountford 2002a, Mountford 2004, Mountford & Ball 2004), and there is a distinct scarcity of oak regeneration throughout lowland Britain (Rackham 2003). This was not altogether surprising where the stands under study remained closed or were only part-opened, given that oak is generally regarded as being rather light-demanding. This is, however, not a simple case of the seedlings requiring high light to survive: oak seedlings (particularly of sessile oak) can persist at rather low light levels under laboratory conditions (Jones 1959, Jarvis 1964, Shaw 1968a). However, in the field they require more light to overcome a range of debilitating factors (see below). Nevertheless, oak also failed to regenerate even where larger canopy gaps developed. It is difficult to pinpoint the causes behind this, but potentially it was connected with its irregularity of seed production, the scarcity of seed-bearing tree (at least at Toy's Hill and Monks Wood), the degree to which acorns are consumed by and rely on animals for dispersal, and the various difficulties that oaklings

encounter whilst establishing and developing (notably insufficient light, insect defoliation, spring frost damage, mildew disease, competition from bracken/bramble, and deer/livestock browsing) (Watt 1919, Jones 1959, Ashby 1959, 1967, Ovington & MacRae 1960, Jarvis 1963, 1964, Ovington & Murray 1964, Tanton 1965, Mellanby 1968, Shaw 1968a, 1968b, 1974, Bossema 1979, Gordon & Rowe 1982, Pigott 1983, Everard 1987, Hilton *et al.* 1987, Evans 1988, Worrel & Nixon 1991, Gurnell 1993, Humphrey & Swaine 1997a, 1997b, Löf 2000, Ouden 2000, Vera 2000). Perhaps the most significant factors involved with the recent failure of oak regeneration are: (i) the arrival of an oak-mildew disease from North America; and (ii) an increase in seed predators, particularly the American grey squirrel (see Pigott *et al.* 1991, Rackham 2003).

Deer certainly played a part in preventing oak from developing in larger gaps at Toy's Hill, though the records available suggested that few oak seedlings ever established, i.e. other factors were probably more important. Deer also played a part at The Mens, as did the vigorous growth of holly, though again no vigorous oak seedlings were ever observed. The clearest indicator that deer and pony browsing prevented oak regeneration was at Denny, where herbivores numbers were abundant and small oak seedlings were observed in gaps, but not saplings. This forms part of a recent widespread failure of tree regeneration across the New Forest, due to an upsurge in large herbivores (Tubbs 2001).

It has been observed or postulated that oak seedlings can be protected from large herbivores and develop in the cover afforded by fallen trees, coarse ground vegetation and prickly plants (Watt 1919, Fenton 1945, Morgan 1987a, 1987b, 1991, Sanderson 1996, Vera 2000). This has been most clearly demonstrated with blackthorn and bramble where herbivores have been moderately abundant or in decline (Kuiters & Slim 2003, Bakker *et al.* 2004). However, the records from Denny Inclosure study site (and from also adjacent unenclosed part of Denny – see Mountford & Peterken 2003) showed that prickly bushes

of holly and bramble were largely destroyed in the face of high herbivore pressure and no regeneration developed. Perhaps the situation would have been different if herbivores had been (much) less numerous, and followed the model suggested by Morgan (1987b) aided by dispersal of acorns by jays (Mellanby 1968, Bossema 1979, Kollmann & Schill 1996). This is also suggested by evidence from the unenclosed part of Denny and from elsewhere (Vera 2000, Rackham 2003), though oak is a highly palatable species and is frequently sought out by large browsing animals (Peterken & Jones 1989, Putman 1994a, Moore *et al.* 1999, Gill & Beardall 2001, Harmer *et al.* 2001).

At the opposite end of the spectrum, the records from this study demonstrated that mature oak trees in natural stands are vulnerable to damage during windstorms. Several mature oak lost large parts of their crown or were completely snapped off or uprooted during severe windstorms. In addition, a large number of oak, most notably at Clairinsh, had a few crown branches or larger boughs snapped out during less severe gales. In fact, crown or trunk breakage (rather than uprooting) was the most prevalent kind of wind damage recorded on mature oak. This was also found to be the case in assessments made of the damage caused across southern England by the 1987 windstorm. Not only was wind damage found to be widespread in oak woodland, but also a high percentage of oak standards were severely damaged. Moreover, oak was most frequently broken or decrowned rather than uprooted, with the latter being mostly associated with stands on sandy soils (see Whitbread 1988, 1991, Grayson 1989, Cutler *et al.* 1990, Peterken 1996). Studies of windstorm damage in 1999 at Suserup Skov and Draved Skov reserves in Denmark also found that oak suffered more from trunk/crown-snapping than uprooting (Bigler 2002a, Bigler 2002b, Emborg *et al.* 2002, Wolf & Bradshaw 2002). The tendency for oak to shed branches or break part way up rather than uproot must be partly related to its deep-rooting capacity (Longman & Couttis 1974). Oak is also much less liable to fungal attack than beech and attacks on oak heartwood by fungi such as *Fistulina hepatica* are

slow (Murray 1974). It was also apparent from the trees recorded at Clairinsh that the irregular crown branching pattern of wood branches plays a part in this.

Despite a number of recorded oak suffering wind damage, several uprooted and many wind-broken individuals started to redevelop. This included a few uprooted trees, notably a large oak at Toy's Hill that developed some strong upright sprouts on the lower trunk and at the base. Nevertheless, most uprooted oak died because they had been weakened by exclusion beforehand, were sheared from their roots, and/or were subsequently shaded. In contrast, many that had been snapped or shed branches sprouted well on the upper trunk and/or crown branches, comparable to regrowth after pollarding (Mitchell 1989), though again this depended on the extent to which trees were subsequently shaded. Rackham (2003) also found that survival of damaged trees 10-15 years after the 1987 storm was generally high amongst top- and bough-broken trees and that survival of uprooted trees was greater for beech than oak or sweet chestnut because of differences in their shade-tolerance. In a study of toppled and snapped trees five years after the storm at Ham Street Woods, Thomas *et al.* (1994) found that less than half of the recorded windthrown oak had survived, whereas three-quarters that had been snapped had. Sprouting was not confined to wind-damaged oak, but also occurred on many undamaged oak at the study sites that were simply released from competition. Comparable patterns of response have been recorded on oak at other reserves (e.g. Mountford *et al.* 2001b, Mountford & Ball 2004) and can be observed widely. In the unenclosed part of Denny, vigorous epicormic sprout growth has developed on large oak released from competition with beech killed by the 1976 drought (Mountford & Peterken 2003). The large oak individuals that had been pollarded or coppiced at Denny, The Mens, Monk's Wood and Clairinsh showed that oak can develop into dominant trees after this type of damage. Indeed, oak generally responds well to pollarding and coppicing and can dominate sites managed by these methods (Rackham 2003). It seems to respond better to pollarding if at least some branches are retained and

the trees are not stressed by drought (Dagley & Burman 1996). Oak trees can respond well to release as induced by silvicultural thinning, even when over 100 years age and having suffered many years of suppression crown. This often involves them developing a sheath of epicormic shoots on exposed parts of the trunk and crown branches, which will develop into large branches if adequately lit (Jones 1959, Evans 1984). The observed tendency for oak to shed branches or snap off high up during windstorms (rather than being uprooted) and recover by sprouting afterwards, gives it a greater degree of resilience to wind damage over beech (one of its major competitors). Given that most of the oldest oak trees known in Britain are outgrown pollards (Tubbs 2001, Rackham 2003), this must represent an important long-term survival strategy in natural stands.

Another factor that affected the long-term survival of mature oak was drought. However, it proved much less susceptible to drought than beech, no doubt helped by its deep-rooting capacity (Longman & Couttis 1974). Even so, the few dominant oak that died unexpectedly or went into severe decline at Denny study site did so after a succession of summer drought years in 1975, 1976, 1989, 1990 and 1995. This formed part of a wave of sudden oak decline reported across lowland England following the drought years of 1989 and 1990 (Gibbs & Greig 1997), and part of a similar decline of oak trees across central Europe associated principally with defoliation and drought or winter/spring frost (Thomas *et al.* 2002). Oak was also largely unaffected by the drought of 1976 at Lady Park Wood, unlike beech and birch (Peterken & Mountford 1996).

Oak characteristically has a prolonged phase of old age and can go living for 500 years or more (Tubbs 2001, Rackham 2003). Certainly the oldest oak trees recorded at Langley, Clairinsh and Denny study sites included trees of 360, 382 and 404cm gbh that seemed to be over 300 years old. Yet there was no indication that such trees were dying from old age, though some had deteriorated or died due to wind or drought damage. Most surviving

mature oak were in fact still growing well in terms of their basal area increment and their crown foliage appeared healthy enough unless affected by exclusion or other factors.

4.2.2.3. Birch

The natural development of birch was recorded across all the study sites in various stand mixtures and on various soil types. The records emphasised that birch can be an abundant and vigorous species in regenerating and young natural stands, especially where large gaps have been created on more acidic soils as happened at Toy's Hill study site following the 1987 storm. Such regeneration was observed in other windblown beechwoods after this event (Whitbread 1991), including on acidic sandy soils to the south of The Mens and acidic clayey soils at Shellem Wood (Mountford 2002a). Birch has also regenerated strongly in large windstorm gaps on acidic soils at Fontainebleau reserve (Pontailler *et al.* 1997). However, the study records also showed that birch is generally intolerant to overtopping and will decline where it faces direct competition with other large trees, notably beech, oak, ash and small-leaved lime. Birch is widely recognised as a pioneer tree of large canopy gaps, particularly (though not exclusively) in more acidic woods, where there is plenty of bare earth and little early competition from ground vegetation. It can colonise *en masse* from a few seed bearing trees: these regularly produces copious amounts of seed that is widely dispersed by the wind and grows vigorously once established. However, birch is strongly light-demanding and, even if it stays well-lit, it will slow in growth after several decades of initial rapid growth (Watt 1923-25, Brown 1953, Ovington & Madgwick 1959, Hamilton & Christie 1971, Miles & Kinnaird 1979a, Harding 1981, Gordon & Rowe 1982, Evans 1984, 1988, Peterken & Jones 1987, Grime *et al.* 1988, Perala & Alm 1990, Rodwell 1991, Atkinson 1992, Peterken 1993a, Cameron 1996, Rackham 2003).

It was notable just how much birch regeneration came up at Toy's Hill despite it being scarce in the former stand. Although some dormant seed might have been present in the area studied when the 1987 storm struck, much of the birch regeneration observed probably developed from fresh seed, blown in shortly before the storm struck (Harding 1981) from trees located some distance away. At The Mens study site, however, it seemed that birch did not come in some 1987 windstorm gaps because seed dispersal was limiting. This might have also been influential in Denny Inclosure. Certainly seed-bearing birch were scarce at these sites and, presumably, birch seed was less widely blown as the stands were more closed than at Toy's Hill.

Despite regenerating strongly at Toy's Hill, birch still failed to establish everywhere. This patchiness appeared to reflect differences in its early establishment as governed by the position of fallen trunks, crown debris, fallen live crowns, holly thickets and bracken. The remaining ground was largely unvegetated (as it had been under a dense beech canopy beforehand) and well lit. This provided very suitable conditions for birch regeneration. At The Mens, a major constraint to birch regeneration in larger windstorm gaps was competition from dense (holly) shrub growth, but other gaps appeared too small or too narrow to provide sufficient light for it to develop. In gaps at Denny, the coarse grassy vegetation that filled many of these may have limited birch establishment. Birch seedlings germinate and develop best on bare ground that is free of vegetation and deep litter and where they remain unshaded, though they can grow through bramble provided they establish before this expands and in gaps between heather plants (Miles 1973, 1974, Kinnaird 1974, Helliwell & Harrison 1979, Miles & Kinnaird 1979a, Pigott 1983, Peterken & Jones 1989, Mountford & Peterken 2000).

Birch would probably have regenerated widely at Denny study site if deer and ponies had been less numerous. It has failed to regenerate in recent times in many New Forest wood

pastures due to an upsurge in large herbivores (Putman *et al.* 1989, Tubbs 2001). Although birch can regenerate in gaps in the face of substantial browsing pressure, it often stops doing this when deer and/or livestock numbers are high. It is a favourite food item of roe deer, and livestock and fallow deer will also eat young birch, though they tend to prefer other species (McVean & Ratcliffe 1962, Kinnaird 1968, 1974, Miles & Kinnaird 1979b, Peterken & Jones 1989, Mitchell 1990, Kay 1993, Putman 1994a, Hester *et al.* 1996, Mountford & Peterken 2000). The latter was apparent in the windstorms gaps at The Mens, where deer browsing had only a small influence on birch regeneration but affected ash seedlings much more, implying that browsing here was mainly by fallow deer.

Well-lit birch recruits grew more quickly than other species. Indeed, the most vigorous birch saplings recorded in windstorm gaps at Toy's Hill and The Mens grew very quickly. The fastest on acidic soils at Toy's Hill attained rates of 1cm dbh and 1m height increment per year, which is about as fast as birch can grow (Evans 1984). Birch saplings were somewhat slower growing at The Mens, probably because they were less well-lit, but still they outstripped the most vigorous ash saplings and by far outstripped all beech saplings. This order of growth is usual (e.g. Peterken & Jones 1989) and gives birch a distinct advantage over other species, but only in large gaps where it is adequately lit.

It was somewhat surprising that (despite proving largely intolerant to overtopping) a good many suppressed birch survived under a birch-oak canopy at Clairinsh. Admittedly, some suppressed birch also survived at Langley under a birch canopy. Perhaps this was because downy birch was the species involved at Clairinsh (though there is no reference to any difference in shade-tolerance in available literature). In addition, it had probably benefited from the partial opening of the canopy here, not only in the 1968 windstorm but also during later windstorms. This was significant because some of the suppressed birch were released where canopy oak were broken and looked like they would fill such gaps.

Unlike beech, only a minority of birch at Toy's Hill were badly debarked by grey squirrels. However, although only a few vigorous poles were affected when the site was recorded in 1998, on a return visit in June 2001 it was found that the situation had worsened with several of the largest birch having had their tops killed by squirrels. Although pole-sized birch in mixed stands are usually less vulnerable to squirrel debarking than beech or sycamore, they are nevertheless commonly attacked (Rowe 1984, Rowe & Gill 1985, Mountford 2002a). Where this does occur, it will put affected birch poles at a major disadvantage in the development of the stand.

Birch is characteristically a short-lived tree in lowland woods and often dies due to senescence, drought, windthrow or fungal attacks before it reaches a hundred years (Rackham 2003), though it lives longer further north (e.g. Kinnaird 1968, Mountford & Peterken 2000). This was apparent in the stands recorded for this study. The largest mature birch, which ranged from 132-172cm gbh, were probably around one hundred years old. Although some of the recorded large birch retained reasonably large, healthy crowns and showed no signs of senescence, some at Langley appeared to have slowed in growth, all the large birch at Monks Wood had been killed by the 1976 drought, and others at Langley and Clairinsh had died after being windthrown. The 1976 drought probably affected birch at other study sites, but this event predated and was not obvious at the baseline recordings. It certainly killed many of the birch in the young-growth stands at Lady Park Wood reserve, especially those growing on shallow soils (Peterken & Jones 1989, Mountford 1994), and also most of the large birch in Cambridgeshire (Rackham 2003). Mature birch have proved vulnerable to windthrow at other reserves (Mountford 1994, Mountford unpublished data) and many were toppled across south-east England in the 1987 windstorm (Whitbread 1991).

Only a few birch recorded at the study sites showed signs of recovering from wind damage. Most uprooted birch died within a few years and none produced vigorous upright shoots. Birch that were broken higher up did, however, occasionally sprout strongly and form new leaders. In addition, several suppressed birch showed signs of release into canopy gaps. This was mainly through crown expansion, but sometimes such trees produced vigorous trunk/crown sprouts. The ability of birch to regrow after breakage was evidenced by the presence of some coppice birch at several sites, though these were infrequent and no birch pollards were observed. Rackham (2003) similarly notes that in east England birch can coppice well, but only on some sites, and that it pollards weakly.

4.2.2.4. Ash

Records of natural changes in ash were made on a range of soils at five of the study sites (Denny, The Mens, Monks Wood, Langley Wood, Clairinsh). They emphasised its: (i) preference for more base-rich and moist soils; (ii) ability to patchily regenerate from seed below small-medium canopy gaps; (iii) capacity to grow rapidly into a tall, reasonably long-lived, dominant tree; and (iv) general intolerance to overtopping and direct competition from other large trees, notably beech and oak – only at Monks Wood, where ash faced little competition from other trees, was it dominant.

Ash is widely recognised as a vigorous species that grows best on moist, base-rich soils. It readily regenerates from seed and regularly produces relatively large numbers of seed, which are dispersed some distance by the wind. Early growth is best on warm, well-watered and nutrient rich sites. Nevertheless, ash seed production can be erratic, the seed is not blown very far, some seed predation occurs, and seedlings often suffer from damping off, competition from ground vegetation and herbivore browsing, and need to be well-lit to grow rapidly. Although ash will grow rapidly, it usually peaks after four to five decades and reaches a maximum height of 18-26m in height (only exceptionally does it exceed

30m). Even on mesotrophic soils it tends to be eventually replaced if growing with beech (Watt 1923-25, Ashby 1959, 1967, Wardle 1961, Hamilton & Christie 1971, Gardner 1977, Flowerdew & Gardner 1978, Helliwell & Harrison 1979, Gordon & Rowe 1982, Helliwell 1982, Evans 1984, Peterken & Jones 1987, 1989, Grime *et al.* 1988, Rodwell 1991, Savill 1991, Peterken 1993a, Mountford 1994, Kerr 1995, Rackham 2003, Kerr & Cahalan 2004).

Most recent ash regeneration recorded at the study sites was associated with small-medium canopy gaps or at least part-broken stands dominated by light crowned trees. At Monks Wood, ash initiated below a part-broken, light canopy dominated by maturing ash and which had various small-medium openings created in it during 1976-96. This allowed many ash seedlings to establish, some of which developed into vigorous saplings. Most ash saplings recorded at Langley developed below a light canopy of mainly birch. These appeared to have survived in a suppressed state for many years, until the canopy opened somewhat and some were released into strong growth. It seemed that this would eventually lead to ash replacing birch at least in the stand recorded on base-rich soils. Ash regeneration as recorded at The Mens study site initiated mainly in and around gaps created by the 1987 windstorm. Such establishment was observed in gaps in other woods after this event (Whitbread 1991) and some of this developed strongly to replace former beech-dominated stands (Mountford 2002a, Mountford 2004, Mountford & Ball 2004).

It was not surprising that most ash regeneration was associated with canopy gaps and improved light conditions. Ash is commonly regarded as a potential filler of gaps on calcareous and mesotrophic soils, especially where the soil is deep and reasonably large gaps are created to provide sufficient light for seedlings. In fact, it commonly develops as small advance regeneration below slightly-opened canopies, though it can struggle to do this under its own canopy where a ground vegetation cover exists. Provided such small

seedlings are at least moderately well lit they will develop upward, though only a few in each group typically make it into strong trees (Watt 1923-25, 1934, Okali 1966, Wardle 1959, Gardner 1975, 1977, Rackham 1975, Evans 1988, Rodwell 1991, Savill 1991, Tapper 1992, 1993, Waters & Savill 1992, Savill *et al.* 1997). Nevertheless, it was apparent from some of the gaps recorded at The Mens (which lacked ash seedlings), that in stands where seed-bearing ash trees have been largely excluded, ash may be unable to effectively establish in places because there is no or only a limited supply of ash seed.

Despite ash initiating in abundance at Monks Wood, muntjac deer destroyed most of this during 1985-96 and presumably prevented canopy gaps filling with some or much ash regeneration in 1996. In addition, only a few of the ash seedlings that established at The Mens developed into strong saplings. There were several reasons behind this: (i) those that developed strongly were certainly reasonably well lit, away from and not checked by dense holly groves, and in places protected from deer browsing, i.e. encircled by holly bushes or amongst bramble or piles of dead wood – the latter was significant as it provided evidence for the model of regeneration described by Morgan (1987b) and extended by Vera (2000), though it should be noted that most of the browsing was probably done by fallow deer and they were not that abundant; (ii) several of the ash that did develop strongly (and perhaps more that left no trace) were killed or badly damaged by vole debarking – it was surprising that ash suffered such damage but no beech saplings did, as voles tend to damage seedlings with an order of preference of beech >oak >ash >birch (Pigott 1985) – however, this might have been because the beech were not as old and tall as the ash; and (iii) many of short, non-vigorous ash seedlings were deer-browsed, though they appeared insufficiently well lit to develop strongly upward anyway – ash is noted as being one of the most palatable broadleaved species (Gill & Beardall 2001, Harmer *et al.* 2001) and is consequently scarce in the New Forest and other wood-pastures (Tubbs 2001, Rackham 2003) – it is particularly prone to browsing by fallow deer and livestock (and judging by the records

from Monks Wood muntjac deer too), especially if growing unprotected (Linhart & Whelan 1980, Peterken & Jones 1989, Mitchell 1990, Kay 1993, Hester *et al.* 1996, Latham & Blackstock 1998, Moore *et al.* 1999, Rackham 2003) – in contrast, roe deer tend to browse birch and oak over ash (Putman 1994a).

Although ash grew and regenerated mainly on ground that had moist base-rich soils, it was striking that at Langley Wood study site some understorey ash saplings and seedlings developed below a birch-oak canopy where the soils appeared relatively dry and acidic. Although this was partly due to an improvement in light conditions within these stands and might have been influenced by an increase in nearby seed-bearing ash trees, it also seemed possible that soil fertility had increased over time correlated with the ability of birch leaves to reduce soil acidity and/or the roots to bring nutrients at depth to the surface (Dimblcby 1952, Gardiner 1968, Miles 1981). Admittedly, ash does grow on more acidic woodland soils, but usually these are loamy, sometimes flushed by ground water, and still relatively fertile and moist (Peterken 1993a, Rackham 2003).

Although many of the ash trees recorded at the study sites were only approaching maturity, it was apparent that such trees could be damaged by the wind. At Monks Wood a few large trees were windthrown, others had large branches snapped out, and several large coppice ash stems or low forks were snapped off. The latter were mainly leaning, poorly attached, and/or had signs of decay or sunken cavities, which are not that uncommon in ash (Helliwell 1982, Evans 1984, Kerr 1995). At Clairinsh both of the recorded large ash were windthrown in the 1968 windstorm, whilst at The Mens the two largest recorded ash had branches or as much as half the crown ripped out in the 1987 windstorm. Observations made across southern England revealed that ash proved moderately vulnerable to damage in the 1987 windstorm, and suffered as much from crown breakage as uprooting, with most breakage resulting in less than 50% crown loss (Whitbread 1991). The tendency for ash to

shed crown branches during windstorms is probably related to its tendency to develop trunk and crown forks, the strength with which these are attached, and its deep-rooting capacity. It was noticeable that a number of ash recorded at the study sites had grown with a forked or distinctly kinked trunk and various crown forks, possibly because leading buds/shoots had been damaged by the larvae of the ash bud moth *Prays fraxinella* or late-spring frost, which can induce forking and irregular trunk development (Gent 1955, Foggo 1996, Kerr & Boswell 2001).

Only a few of the recorded ash that were uprooted by the wind remained alive and produced trunk shoots. However, a good many that had only part of the crown snapped out responded by sprouting high up in a pollard-like form. Other ash that were released beside gaps responded by producing sprouts usually combined with increased crown growth. Although ash will pollard well (Rackham 2003) and the very largest ash tree recorded at Monks Wood study site had developed a pollard-like form, the survival of such trees depends on them not being too heavily shaded and, as Evans (1984) remarks, once the crown of an ash is constrained it is not easily increased again when released. The ability of ash to regrow from (cut) stumps was clearly evidenced by the numerous ash stools that were recorded at Monks Wood, as is a common feature of the species (Rackham 2003). However, it remains unclear if this will be an effective means of recovering in natural stands after uprooting.

Ash is not an exceptionally long-lived tree, usually lasting for two or perhaps three centuries at most (Wardle 1961, Rackham 2003). Unfortunately, there were too few records from the study sites to test this in natural stands in lowland Britain. Monks Wood was the main site where mature ash were recorded, but these were probably only about 100-150 years old and showed no major signs of crown deterioration due to senescence.

4.2.2.5. Small-leaved lime

Small-leaved lime was recorded only at Langley Wood study site where it grew on moderately acidic, brown earth soils. It proved to be a vigorous tree producing many tall, straight, coppice poles and excluding nearby stems of other species. It was not as fast growing as the fastest contemporary birch, but it still grew rapidly and was far more tolerant of shade and excluded most nearby birch. It also had a scatter of saplings recruit and develop steadily below nearby birch. Small-leaved lime is recognised mainly as a tree of ancient coppice woodland. It is capable of developing into a canopy tree on a variety of soil types, though it is frequently found on acidic loamy soils. Dominant lime stems usually grow rapidly and straight, achieving 20m in height and 30cm diameter in 50 years. Individuals are capable of maintaining vertical growth down to light transmission levels as low as 10%, and readily persist as an understorey to light crowned trees. Only on deeper loams does it face strong competition from beech. No large trees were recorded at the study sites, but it is potentially long-lived and capable of growing to over 30m high and 200cm diameter (Pigott 1988, 1989a, 1989b, 1991, Peterken & Jones 1987, 1989, Rodwell 1991, Peterken 1993a, Mountford 1994, Rackham 2003).

No lime seedlings were recorded below the stands at Langley, but some were reported to have developed in the 1980s, only to be eaten by deer. Lime can form as advance regeneration in fairly shady conditions and develop in small-gaps, but its dispersal capacity is rather short, it relies on warm daytime temperatures in late July and early August for effective seed ripening, wood mice and bank voles readily consume fallen lime seeds and seedlings, the young growth is vulnerable to debarking by bank voles, and low growth of lime is frequently browsed by deer and other large herbivores (Pigott 1975, 1985, 1991, Pigott & Huntley 1981, Peterken & Jones 1987, Rackham 2003).

The lime recorded at Langley suffered very little wind damage, save for a few substratum stems that were indirectly broken by wind-snapped oak or birch. However, the lime here were not that old and no doubt larger lime trees would be more vulnerable to wind damage, though it is generally deep-rooted (Cutler *et al.* 1990, Pigott 1991) and presumably less vulnerable to uprooting than shallow-rooted species such as beech. In addition, recorded lime stems that were broken very often sprouted near the break and released trees readily expanded into gaps. In fact, lime shows a remarkable (almost indefinite) capacity to regenerate from stump sprouts, will readily layer from pinned branches, and often regrows after being broken, toppled, pollarded or snapped high up (Koop 1987, Pigott 1991, Peterken 1996, Rackham 2003, personal observation). As such, lime can be expected to redevelop into canopy a tree or even persist in a pollard-like form after being wind-damaged, provided other conditions are not limiting.

4.2.2.6. Field maple

The natural development of field maple was recorded at three of the study sites (Monks, The Mens, Langley Wood) where a range of soils occurred. The records emphasised its: (i) preference for more alkaline and circum-neutral, base-rich, clayey brown earth soils; (ii) capacity to grow into a medium-tall, reasonably long-lived tree; (iii) relatively slow growth and intermediate tolerance to overtopping; and (iv) limited capacity to regenerate from seed below small-medium canopy gaps.

Field maple was most abundant and grew best on calcareous, base-rich clayey soils under a light canopy of ash at Monks Wood study site. It commonly does this in ancient woods in eastern England and elsewhere in the English lowlands (Rodwell 1991, Peterken 1993a, Rackham 2003). At The Mens and Langley Wood study sites it persisted in the substratum in places, but was much less abundant than at Monks Wood. This appeared to be partly due to the soil conditions: it tended to occur only where the soils were somewhat more clayey

and base-rich, as it does other woods with more acidic soils (Rackham 2003). In addition, it certainly struggled more under the heavier canopy of beech and oak than ash. Indeed, field maple normally persists only in small numbers as a subordinate tree or understorey shrub in most mature beechwoods and mainly on calcareous soils (Jones 1944, Peterken & Jones 1987, 1989, Rodwell 1991, Peterken 1993a).

Where field maple was represented at the study sites, it hardly recruited below closed or part-broken stands or in larger gaps, despite the seedlings being quite shade-tolerant (Jones 1944). At The Mens and Langley Wood, this must have been partly related to the scarcity of seed-bearing field maple trees combined with its rather irregular seed production (Jones 1944). This can have hardly been the case at Monks Wood where medium-large field maple were quite numerous. Nevertheless, it is not uncommon to find ash rather than field maple seedlings coming up in such woodland: even those field maple seedlings that do come up are slow growing and moderately vulnerable to deer browsing (Jones 1944, Peterken & Jones 1989, Rackham 2003).

Although the main field maple population at Monks Wood was not that old, a few large trees were windblown and several others had branches or major parts snapped out. Most that were toppled died, but some that were snapped higher up produced sprouts. Larger-scale surveys have found that field maple tends to suffer more from trunk breakage than uprooting during windstorms (Whitbread 1991), which combined with its ability to grow in a pollard-like form (Rackham 2003) could help to maintain in stands affected by wind damage. Although it readily regrows from stump sprouts after coppicing, it remains unclear if such sprouts could regenerate individuals that have been uprooted or broken near the ground during windstorms.

Field maple trees seem to be capable of living for at least 200-300 years (Jones 1944, Rackham 2003). Certainly, the largest recorded field maple of 130-160cm gbh at Monks Wood study site were probably over a hundred years old and showed few signs of obvious deterioration due to old age. Nevertheless, some were in a poor state or had died. This may have been due to early senescence, but it seemed that other causes were more likely, possibly the effects of prolonged drought combined with exclusion.

4.2.2.7. Holly

Records of the natural development of holly were made mainly on acidic-mesotrophic brown earth or stagnogley soils at Denny, The Mens, Clairinsh, Toy's Hill and Langley Wood. No holly was recorded on the alkaline clayey soils at Monks Wood, and it hardly occurred on base-rich or wet ground at Clairinsh and Langley. The records emphasised its: (i) ability to develop into a long-lived, medium-tall bush or tree; (ii) regenerative capabilities within relatively shady conditions; and (iii) ability to expand strongly once released. The expansion of a dense holly understorey was one of the notable features recorded at Denny, The Mens and Clairinsh.

The above aspects are recorded more widely across Britain in semi-natural woodland (Watt 1934, Tansley 1939, Peterken & Lloyd 1967, Rodwell 1991, Rackham 2003). Holly is widespread and occurs in many woodland types. It is often prominent as a slow-growing, shade-tolerant understorey shrub or sometimes as a medium-tall tree below mature beech-oak stands and gaps therein. However, it is generally less abundant in drier areas, such as the Chilterns, and is limited by prolonged winter frost – hence it is less common in continental woods (Jahn 1991).

Holly developed at the study sites in three main ways: (i) as low-growth around established bushes, spreading from shallow root suckers and low layering branches; (ii) from more

widely dispersed seedlings; and (iii) by sprouting and shooting vigorously once released in gaps (including from stems that were snapped or crushed by falling trees and branches). These traits have been recognised in other situations, and also that holly benefits from its seeds being dispersed by birds (Peterken & Lloyd 1967, Tubbs 2001, Rackham 2003). It was notable that holly invaded much more weakly at Langley Wood study site, where there was no established holly to start with and only a limited seed sources.

Holly was found to have invaded more strongly under certain conditions, i.e. below a mature canopy of birch and oak at Clairinsh, below oak in mature beech-oak stands at Denny and The Mens, and in both where light was increased below gaps. Although it has a high shade-tolerance, it clearly established and grew better was it was not too heavily shaded. It might also have benefited from more fertile soil conditions associated with oak and birch rather than beech (e.g. Ovington 1953-56). The tendency of holly to come in below oak has been reported by others (Tubbs 2001, Rackham 2003). The expansion of holly was particularly impressive in windstorm gaps at The Mens study site: much the same happened at the nearby and similar site of Ebernoe Common and, to a lesser degree, in other woods damaged by the 1987 storm (Whitbread 1991, Mountford 2004, Mountford & Ball 2004).

Holly regeneration was in fact partly hindered by deer browsing at The Mens, but this was trivial compared to destruction of holly after the mid-1960s at Denny study site. In the first half of the 20th century and up to 1964, holly had been expanding in the face of moderate-low browsing pressure in the Inclosure and also the unenclosed part of Denny (see Mountford & Peterken 2003). No doubt the prickly adult foliage of holly facilitated this and also accounts for its general association with wood-pasture sites (Rackham 2003). But this did little to save it at Denny once deer and ponies became numerous. In an analysis of the stand structure of extant New Forest wood pastures, Morgan (1987b) developed a

model of regeneration and predicted that holly would tend to be immune to changes in the intensity of browsing in the New Forest. The evidence from Denny Inclosure (and also the unenclosed part of Denny) contradicts this: excessive browsing has largely destroyed low holly growth and debarking has left many mature holly trees dead or in decline.

Several large holly were recorded at the study sites, including trees of 99cm gbh at Denny and 140-155cm gbh at Clairinsh. These were possibly around 200 years old, given their slow rate of growth, and looked quite capable of growing for much longer (at least if not debarked by deer and ponies). This supports other evidence that suggests or shows that holly can live for 300 years or more (Peterken & Tubbs 1965, Peterken & Lloyd 1967, Tubbs 2001, Rackham 2003).

4.2.2.8. Hazel

The natural development of hazel was recorded at four of the six study sites (The Mens, Monks Wood, Langley Wood, Clairinsh) in various stand mixtures and on a range of soil types. The records emphasised its: (i) predominance on calcareous clayey and more base-rich acidic brown earth soils; (ii) ability to grow into and persist as a multi-stemmed, medium-tall shrub; (iii) intermediate tolerance to shading; and (iv) ability to maintain or expand itself by sprouting, layering or from seedling regeneration.

Hazel characteristically grows as a multi-stemmed bush in across Britain, and especially in ancient semi-natural coppice woods. It is often abundant on more calcareous soils with a moderate to high clay content, but extends on to rather infertile acidic, sandy sites and even wet soils. Nevertheless, hazel is sensitive to shading by overstorey trees, especially those that cast a heavy shade, though that stools can persist for many decades despite being overtopped (Watt 1923-25, 1934, Rodwell 1991, Peterken 1993a, Rackham 2003).

Amongst the study sites, hazel persisted best at Monks Wood where it grew on calcareous clayey soils and was largely under a light-canopy of ash. In areas in this wood where field maple dominated the overstorey, hazel struggled much more because it was more heavily shaded. In addition, several old hazel stems and stools at Monks Wood developed extensive decay and die back, which appeared to be connected with a combination of prolonged shading and possibly a run of dry years and/or infestation by honey-fungus as described by Rackham (2003). Hazel also remained prominent at Langley Wood on moderately acidic soils where it was part-shaded mainly by oak or birch. However, it was absent under areas where lime was dominant, as the shade here was much more intense. At Clairinsh, hazel struggled where it grew on acidic soils and oak closed over it, whereas in open stands on moist, base-rich soils it persisted much better. Although hazel grew on suitable mesotrophic clayey soils at The Mens, it was strongly suppressed by the shade of beech. Similar trends have been recorded at Lady Park Wood reserve, with hazel surviving rather better under canopies dominated by ash and birch than by oak, lime and/or beech (Peterken & Jones 1987, 1989, Mountford 1994, Mountford unpublished data).

Hazel demonstrated a remarkable ability to 'self-coppice' at several of the study sites. Although large old stems of hazel tended to die off or collapse after several decades of growth, exacerbated by their tendency to naturally lose apical dominance and arch over and increased vulnerability to strikes by falling branches or trunks, such stems were frequently replaced by new erect sprouts. These developed most vigorously where bushes were released in gaps. Often they came from the stool base, but they also developed higher up and particularly along larger leaning stems. This characteristic has been observed in other reserves, notably Lady Park Wood (Mountford unpublished data), and can be observed on neglected hazel stools in coppice woods (Rackham 2003). It represents a major strategy in natural stands, which allows established hazel bushes to prolong their lifespan and fill gaps once released.

Regeneration of new hazel individuals was rather limited across the study sites. Some new hazel regenerated below small gaps at Langley and Clairinsh, but few did at The Mens or Monks Wood despite the presence of canopy gaps and mature hazel being numerous at Monks Wood. Most recruits came from seedlings, but a few developed from layered branches, which rooted rather readily. Two key factors behind the scarcity of seedling regeneration were shading (which greatly reduces hazelnut production) and predation of nuts by grey squirrels. This was certainly the case at Monks Wood (Steele & Schofield 1973), but must apply to the other study sites and other woods (see Rackham 2003), except that there were no grey squirrels at Clairinsh. Shading would also have affected any hazel seedlings that did develop (Sanderson 1958), and no doubt the dense holly growth that developed at The Mens and Clairinsh would have hampered any hazel seedlings. On top of this, deer browsing played a role in checking hazel regeneration, with most of the few hazel seedlings recorded at The Mens (and also sprouts on established hazels) being deer browsed. Deer were no doubt a factor at Monks Wood: muntjac deer debarked many small hazel stems and ate most low hazel growth, not only in the study transects but in coppice plots elsewhere in the wood (Cooke 1994, Cooke & Farrell 2001). Hazel is highly palatable to large herbivores, including fallow and roe deer, horses and cattle, and is consequently a scarce component of heavily browsed wood pastures (Putman 1994a, Tubbs, 2001, Rackham 2003).

4.2.2.9. Hawthorn

Records of the natural development of (midland and common) hawthorn were made at The Mens, Monks Wood, Langley Wood and Clairinsh in various stand mixtures and on a range of soil types. They emphasised its: (i) predominance on calcareous clayey and more base-rich acidic brown earth soils; (ii) ability to grow into a multi-stemmed shrub or medium-tall tree; (iii) intermediate tolerance to shading; and (iv) ability to maintain or expand itself by sprouting, layering or from seedling regeneration.

Hawthorn is a characteristic short tree or shrub of deciduous British woodland. It occurs across a wide-range of soil types, but avoids strongly acidic soils. The species as a whole has a strong capacity to resprout and regularly produces seeds that are widely dispersed by birds. However, it is easily overtopped and suppressed by other trees, though common hawthorn can withstand some shading and midland hawthorn even more (Rodwell 1991, Peterken 1993a, Rackham 2003). This was evident from the areas recorded in this study, with hawthorn persisting well (and better than hazel) at Monks Wood where it was largely under a light-canopy of ash and where midland and hybrid hawthorn individuals were widespread. Midland hawthorn was also present at The Mens, where the species managed to persist under a heavy canopy containing much beech. In Lady Park Wood and Buckholt Wood reserves, where the species is represented by common hawthorn, it has proved much less tolerant to shading by beech (Peterken & Jones 1987, 1989, Mountford 1994, 2003, Mountford unpublished data). At Langley, only common hawthorn was present and this proved as or less tolerant of shading by oak and birch than hazel. The same applied to hawthorn at Clairinsh, where common hawthorn persisted primarily as part a mixed understorey in open stands.

Differences were also observed in the form of midland and common hawthorn across the study sites. Midland hawthorn tended to be less upright and smaller-crowned, reflecting its tendency to develop as a multi-stemmed bush of floppy habit (Rackham 2003), whereas common hawthorn tended to develop more as a stout, upright, forked, short tree or stool with a few or (more rarely) several major stems. It seems likely that midland hawthorn stems are less long-lived than common hawthorn, which can grow into trees and reach at least 300 years old (Rackham 2003).

Hawthorn demonstrated several mechanisms by which it expanded or regenerated at the study sites. It generally responded well to release in gaps, through a combination of crown

expansion and by the production of low trunk shoots and side-forks. Broken stems also often sprouted in a similar manner. Fallen stems typically sprouted along the trunk and at the base. In several cases fallen stems regenerated by layering. Hawthorn also had some seedlings establish (notably at Langley Wood), no doubt aided by the dispersal of its seed by birds. Recruits established most strongly where they were well-lit. Sometimes they suffered from deer browsing, though they were given some protection by sharp spines that developed along the stems. These normally protect all but the youngest growth of hawthorn and are a valuable attribute as hawthorn is highly palatable to deer and other livestock (Rackham 2003). Hawthorn hardly regenerated from seed or layers at Monks Wood despite it being frequent as a mature bush and the development of several gaps. This was most likely due to muntjac deer: they ate the few recorded hawthorn seedlings in 1985 and by 1996 had debarked many established small hawthorn stems.

4.2.2.10. Rowan

The natural development of rowan was recorded only at Clairinsh study site, save for a couple of rowan recorded in the beech woodland at Toy's Hill. This was not surprising as rowan is relatively scarce in south-east Britain, but can be rather abundant in ash, oak and birch woodland in north and west Britain where it often grows as understorey tree (Rodwell 1991, Peterken 1993a, Rackham 2003).

The study records emphasised the ability of rowan to invade and develop as a small-medium tall, shade-tolerant, understorey tree mainly below an oak-birch canopy on acidic brown earth soils (though it also extended on to ground with moist base-rich soils). It was protected from browsing by large herbivores on the island at Clairinsh, without which it would undoubtedly not have developed as strongly as it did. It is often browsed or debarked by deer and livestock and is scarce in woods which they access (McVean & Ratcliffe 1962, Kinnaird *et al.* 1979, Pigott 1983, Hester *et al.* 1996, Mountford &

Peterken 2000). It also benefited from the partial opening of the canopy, which allowed released several well-established rowan trees into vigorous upward growth and no doubt facilitated many other members of the population though this was less apparent.

Rowan used several mechanisms to regenerate on Clairinsh. Many recruits developed from seed, which had obviously been spread widely by birds. The initial population of rowan, however, appeared to have grown mostly from stump sprouts, and several prostrate and a few snapped rowan stems regenerated by sprouting at the base and/or high-up. This demonstrated that vegetative regeneration could be a significant component of rowan regeneration in natural stands.

The largest standing rowan recorded at Clairinsh was 95cm gbh, at least 85 years old and still vigorous. Although there was no obvious sign of senescence affecting this or other mature rowan trees, it is reportedly a rather short-lived species lasting for only about 150 years (Grime *et al.* 1988).

4.2.2.11. Alder

The natural development of alder was recorded only at Clairinsh and Langley Wood study sites, though the latter had only two alder trees present. The records showed that alder: (i) had a strong affinity for moist or wet ground, especially with base-poor soils (though it had expanded onto somewhat drier ground and grew on more base-rich soils); (ii) developed into a fairly tall, but not very long-lived tree from coppice, particularly because it declined strongly in the face of competition from oak; (iii) survived better in low-growing stands where canopy shading was less intense; and (iv) formed only a few recruits in open stands and mainly regenerated from basal sprouts, which proved persistent even on large trees.

Many of these facets were not surprising. Alder is a characteristic tree of wet soils across most of Britain, though it is intolerant of stagnant soil water conditions (Rodwell 1991, Peterken 1993a, Rackham 2003). Its seeds are dispersed efficiently by water and to some extent by wind. Although alder can grow on relatively dry ground, its seedlings require moist conditions to establish (McVean 1953, 1956). Alder coppices very readily, but is a light-demanding species that is excluded by most other tall trees. For example, Tapper (1993, 1996) recorded the natural replacement of alder in mixed stands by ash.

Alder is also a relatively short-lived tree, usually making only about 100-150 years before dying (McVean 1953). The largest trees recorded at the study sites measured only 98-111cm gbh. Although they remained healthy (save for the effects of exclusion), they were probably under a century old. A few mature alder were, however, wind-snapped. This form of damage is characteristic, as alder usually develops a deep root system that is rather resistant to uprooting (McVean 1956, Bigler 2002a, 2002b, Wolf & Bradshaw 2002, Wolf *et al.* 2004). Presumably, such individuals could easily re-establish from stump sprouts and there was some evidence from Clairinsh study site to show this is possible, provided the regrowth is adequately lit. This might form a major mechanism by which alder regenerates in natural stands, particularly in alder-dominated stands and where windstorms open large gaps. However, in mixed stands on drier soils alder could well have been largely excluded by other species beforehand.

4.2.2.12. Grey willow

Grey willow was abundant as a medium-tall, multi-stemmed shrub growing on shingle by the loch edge at Clairinsh study site. It seemed capable of perpetuating itself almost indefinitely by layering into the shingle from collapsed individuals or stems. Even so, it was unable to extend far onto to the island where taller growing birch, alder and ash took over. These features are commonly observed around stretches of open water, with willow

being particularly tolerant of heavily waterlogged soils and rooting readily from detached branches and twigs, but being intolerant of competition from taller trees (Tansley 1939, Rodwell 1991, Grime *et al.* 1988). These characteristics give it a rather specialised place within native woodland stands.

4.2.3. Synthesis & comparison of the natural development of major woodland types

In this section, the long-term natural development of the major native woodland types represented at the study sites is considered. This is based on the main trends recorded at the study sites (as summarised in Table 4.1 and detailed in Sections 3.1-6), and the ecological profiles established for each species as detailed in Sections 4.2.2.1-12.

4.2.3.1. Natural development of mixed beech stands (in southern Britain)

The main trends recorded in naturally developing mixed beech stands in southern Britain on moderately acidic, mesotrophic to base-poor, clayey stagnogley/brown earth soils at Denny, The Mens and Toy's Hill study sites are given in Table 4.1. They emphasise the potentially dominant role that beech and holly can have, particularly where disturbance remains small-scale and other factors (notably browsing and grey squirrel debarking) are not limiting for them. Where larger-scale disturbances occur, notably due to severe drought and windstorms, then it is likely that birch, ash, oak, hazel, hawthorn and various other species will be form part of the stands.

These trends show consistencies with other records from minimum-intervention beech woodland reserves in Britain: (i) the main trends recorded in closed stands, prevention of beech, holly and other regeneration by large herbivores (except mainly in exclosures), set back of mature beech and oak by wind damage, and set back of pole beech by grey squirrel debarking has been similar at Dendles Wood (Mountford *et al.* 2001b); (ii) the main trends recorded in and below closed stands, and set back of pole beech by grey squirrel debarking

Table 4.1: Summary of the species development and main trends in each of the major native woodland types recorded at the six study sites

Study sites	Denny, Toy's Hill, The Mens	Monks Wood	Langley Wood	Clairinsh	Clairinsh, Langley Wood
Type of woodland represented [main equivalent type in NVC [a]]	Mixed beech woodland in southern Britain [W14/W15]	Mixed ash woodland in southern Britain [W8]	Mixed oak-lime woodland in southern Britain [W10]	Mixed oak woodland in northern Britain [W11]	Wet woodland [W2/6/7]
Major species recorded	Beech, oak, birch, holly, ash, hawthorn, hazel	Ash, oak, (birch), field maple, hawthorn, hazel, various shrubs	Oak, birch, small-leaved lime, hazel, hawthorn	Oak, birch, holly, rowan, hazel	Willow, birch, ash, alder, oak, various shrubs
Main soils recorded	Moderately acidic, mesotrophic to base-poor, clayey stagnogley/brown earth	Calcareous, base-rich, clayey brown earth	Moderately acidic, base-poor, clayey-sandy stagnogley/brown earth	Moderately acidic, base-poor, stagnogley/brown earth	Base-poor & moderately base-rich stagnogley/gley
Main trends recorded in closed stands	Exclusion of ash, birch, oak, hawthorn and hazel more than beech and holly Well-established canopy oak remained competitive Weak understorey of hawthorn & hazel persisted in places Holly & beech persisted & developed in understorey	Exclusion of birch, oak, hawthorn & hazel more than ash Well-established canopy oak remained competitive Field maple, hawthorn, hazel & various shrubs persisted in understorey	Exclusion of birch, oak, hawthorn & hazel more than lime Well-established canopy oak & birch remained competitive Hazel & hawthorn & some other species persisted in places in understorey	Exclusion of birch, hazel and oak more than holly & rowan Well-established canopy oak & birch remained competitive Weak understorey of hazel persisted in places Holly & rowan persisted & developed in understorey	On stagnogley soils, alder, ash, birch, willow & various shrubs tended to be excluded by well-established canopy oak – at one site ash developed below and part-replaced birch, whilst on another site holly & rowan developed in understorey On gley soils, mixed-species, open, shrubby stands tended to persist

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Table 4.1: continued

Study sites	Denny, Toy's Hill, The Mens	Monks Wood	Langley Wood	Clairinsh	Clairinsh, Langley Wood
Type of woodland represented [main equivalent type in NVC [a]]	Mixed beech woodland in southern Britain [W14/W15]	Mixed ash woodland in southern Britain [W8]	Mixed oak-lime woodland in southern Britain [W10]	Mixed oak woodland in northern Britain [W11]	Wet woodland [W2/6/7]
Main species recorded in mature stands	Beech & oak in overstorey Holly, beech, (hawthorn) & (hazel) in understorey	Ash & oak in overstorey Field maple, hawthorn, hazel & ash in understorey	Oak, small-leaved lime & birch in overstorey Hazel & hawthorn in understorey	Oak & birch in overstorey Holly, rowan & hazel in understorey	On stagnogley soils, oak, birch, (ash), & (alder) in overstorey, & ash, holly & rowan in understorey On gley soils, willow, birch & alder, or ash, oak, alder & various shrubs in low stands
Main species recorded/likely to benefit from small-scale disturbance	Holly, beech, (ash), (hawthorn), (hazel)	Ash, field maple, hawthorn, (hazel)	Small-leaved lime, (ash), (hazel), (hawthorn)	Holly, rowan, (hazel), (birch)	Holly, rowan, (ash), (birch)
Main species recorded/likely to benefit from larger-scale disturbance	Birch, ash, oak, hazel, hawthorn, various other species	Ash, birch, hawthorn, hazel, various other species	Birch, ash, oak, hazel, hawthorn, small-leaved lime, various other species	Birch, oak, hazel, various other species	Willow, birch, ash, alder, oak, various shrubs
Main disturbances	Mature beech and (less so) oak set back by drought Mature beech and oak set back by wind damage Pole beech and (less so) birch set back by grey squirrel debarking Understorey stems set back by falling trees & branches Understorey holly & beech destroyed by deer & ponies	Few mature ash & field maple set back by wind damage Birch and possibly hazel and field maple set back by drought Understorey stems set back by collapse and falling trees & branches Ash regeneration & small stems of many species destroyed by deer	Mature oak partially set back by wind damage Mature birch set back by wind damage and possibly drought Understorey stems set back by collapse and falling trees & branches Pole beech & sycamore set back by grey squirrel debarking	Mature oak, ash & birch set back by wind damage Understorey stems set back by falling trees & branches	Mature oak, birch, ash & alder partially set back by wind damage Understorey stems set back by falling trees & branches Trees/shrubs set back by wave erosion

[a] based on the National Vegetation Community types in Rodwell (1991)

has been similar at Buckholt Wood (Mountford 2003); (iii) the main trends recorded in mature closed stands, partial set back of mature beech by drought, and widespread set back of pole beech by grey squirrel debarking in younger stands has been similar at Lady Park Wood – it is worth noting that in old stands lime has proved fairly competitive with beech, whilst in younger stands pole birch was strongly set back by drought and ash and (in places) lime and oak look set to become the main long-term dominants rather than beech (due to squirrel debarking) (Peterken & Jones 1987, 1989, Mountford 1994, 1997, Peterken & Mountford 2002, Mountford unpublished data); and (iv) the main trends recorded in large gaps following severe windthrow of beech have been similar at Noar Hill Hanger and Ashford Hanger, though on the calcareous soils at these reserves the main regenerant has been ash, with some elder, hawthorn and hazel, and small amounts of other species, and in some places gaps have filled mainly with bramble and clematis (Mountford 2004, Mountford & Ball 2004, Mountford & Groome 2004).

Similar trends have also been recorded in and below closed stands, in canopy gaps, and with beech, oak and other species having been set back by windstorms at various other minimum-intervention reserves in continental north-west Europe, including: (i) Pijpebrandje and Het Rot (Netherlands) (Clerkx *et al.* 2000, 2001, Wijdeven 2003b); (ii) Neuenburger and Hasbrucher Urwald (north German coast) (Koop 1981, Wijdeven 2003c); (iii) Fontainebleau (north France) (Koop & Hilgen 1987, Pontailler *et al.* 1997, Wijdeven 2003a) – except that holly is scarce (partly because of deer browsing, personal observation); and (iv) Suserup Skov (Denmark) (Emborg 1995, Emborg *et al.* 1996, 2002) – except that holly is absent because of winter cold.

Some aspects of the trends recorded at the study sites are apparent more widely in other semi-natural beechwoods in lowland Britain (Rodwell 1991). Mature stands are generally dominated by beech with oak occasional, except on strongly acidic sites where beech tends

to be less vigorous and oak is more often co-dominant. Birch and (on mesotrophic soils) ash and other trees are usually scarce, though these may persist in gaps for some time. Often there is a second tier of holly with a little yew, especially in oceanic regions, albeit holly is susceptible to browsing. In addition a little rowan can be found and, on mesotrophic soils, a little hawthorn and hazel and perhaps other species.

The replacement of mixed deciduous oak-lime-hazel woodland by beech-dominated woodland forms part of a long-term regional trend over the last 5,000 years (see Godwin 1975, Küster 1997, Björse & Bradshaw 1998, Bradshaw & Holmquist 1998, Lindbladh *et al.* 2000, Vera 2000), including much of the New Forest where many oak-dominated woods have become beech-oak woods, and oak-dominated woods have become confined (Barber 1975, Flower 1980, Tubbs 2001). This appears to be connected with climatic change (Huntley *et al.* 1989), secondary succession after abandonment of cultivated fields (Godwin 1975, Küster 1997), treatment as wood-pasturage, selective felling and burning (Baker *et al.* 1978, Björkman & Bradshaw 1996, Hannon *et al.* 2000, Cowling *et al.* 2001, Tubbs 2001, Rackham 2003). At Denny, The Mens and Toy's Hill study sites it occurred after a history of wood-pasturage and associated treatment, and subsequently when the sites were enclosed, allowed to natural regenerate, and develop as high forest over many decades. This favoured beech and reduced or eliminated other original-natural species (see Sections 4.1.1.1, 4.1.2.2).

Although the long-term fate of such woodland left to natural development remains open to some speculation and no single outcome can be expected, there are some signs that beech and holly will not become overwhelmingly dominant. They are most likely to do this where canopy disturbance remains small-scale, browsing is limited, and the soils are suitable for their growth (see Sections 4.2.2.1, 4.2.2.7 for details). This will maximise the time that beech can compete directly with other trees in the overstorey and present

substantial opportunities for both species (but not more light-demanding species) to regenerate and fill gaps, accepting that beech can struggle to regenerate from seed below its own canopy. Conversely, large-scale canopy disturbance as caused by severe drought and windstorms, to which beech proved vulnerable, is likely to favour more light-demanding trees and shrubs, especially birch and ash and various shrubs that can readily colonise large gaps. This was highlighted by the changes recorded at Toy's Hill. Moreover, well-established canopy oak proved competitive with beech, were less vulnerable to severe drought, more resilient to wind damage (they tended to remain standing and recovered by sprouting), responded strongly to release, and appeared capable of out-living beech by several centuries. At Denny, there were several examples where mature beech had fallen away due to drought and windstorms and released oak into vigorous growth.

In addition, sustained heavy browsing at Denny destroyed beech regeneration and removed dense patches of holly: now that large gaps have developed this has improved the chances for birch, oak and ash to regenerate if browsing declines. Past records of regeneration in Denny Inclosure and the unenclosed part of Denny (Mountford & Peterken 2003) suggest that the greatest chance for these species to regenerate will be if browsing declines substantially. However, unless they regenerate rapidly they could soon face strong competition from holly, which appears to commonly develop into dense thickets in beechwoods suddenly released from wood pasturage (Peterken 1969, Tubbs 2001, Rackham 2003). With moderate browsing it is possible that holly and bramble could protect tree regeneration from herbivores as proposed by Morgan (1987b), Sanderson (1996) and Vera (2000). To some extent this is supported by the observations made at The Mens, and also given that there are a few vigorous oak seedlings in bramble patches in the unenclosed part of Denny. However, at no time at Denny has there been a striking tendency for tree saplings to grow in association with holly scrub, and the records certainly do not support the view of Morgan (1987b) that 'there will be a base level of regeneration

determined by the relative importance of protective understorey, which will tend to be immune to changes in the browsing regime' – recent browsing has in fact destroyed both potential regeneration and most holly.

The potential role of species other than beech and holly has to be offset against the widespread failure of oak to effectively regenerate from seed in recent times. Even so, there are examples of a few saplings developing in gaps after the 1987 storm (e.g. Mountford 2002a, Mountford 2004, Mountford & Ball 2004), it still regenerates well in some places (Rackham 2003, personal observation), and the potential long lifespan of mature oak trees means it has a greater window of opportunity in which to produce vigorous saplings. Nonetheless, oak may regenerate less abundantly in the future due to the presence of oak-mildew disease from North America (Rackham 2003) and an increase in seed predation by grey squirrels (Pigott *et al.* 1991). Other species, particularly ash, birch, hawthorn and hazel, may be constrained by the scarcity of seed-bearing trees/bushes in mature stands, particularly if such stands fail to break-up early. Birch is disadvantaged over ash because it is shorter-lived, is more sensitive to shading and vulnerable to drought and wind damage, and does not form advanced regeneration. However, it produces more seed which is dispersed further and consumed less, tends to suffer less from deer and bank vole damage, and has saplings that are less-frost sensitive and faster growing.

Thus, it seems possible (though see next paragraph) that in places beech will advance against birch, ash and oak for 150-300 years, but mature trees may then suddenly decline due to severe drought or windthrow, leaving a scatter of oak with an opportunity to grow into veteran trees, particularly as pollard-like trees, and large gaps in which birch, ash, oak and various other light-demanding species have an opportunity to regenerate and grow vigorously, probably amongst holly and some hawthorn, hazel and other species. However, subordinate beech may partially replace mature beech that are lost, some toppled and

broken beech are likely to survive, and beech saplings can be expected to develop as an understorey and replace any birch, ash or oak that develop, facilitated by drought-induced mortality of birch. In addition, it seems possible that in places holly might block tree regeneration and form long-lived thickets. A good deal of the shrub regeneration at least could develop from sprouts rather than seed.

This position has, however, been greatly changed by the arrival of the American grey squirrel. Debarking by this species poses a major threat to the future development of beech poles into replacement canopy trees. Many pole beech have already been badly deformed or killed and more will surely follow suit. Those that do survive seem unlikely to grow as large or last as long their predecessors. Amongst the other three main tree species, ash has proved least vulnerable to debarking. This suggests that beechwoods may well develop with much less beech and much more ash than previously expected.

It is possible that beech-oak woodland could be invaded particularly by sycamore (this has already happened in several woods (Rodwell 1991) and was happening at Denny Inclosure in the 1950s before ponies/deer destroyed the sycamore saplings that had established). However, the chances of sycamore succeeding or persisting where it has established have also been much reduced because it too is frequently debarked by grey squirrels.

4.2.3.2. Natural development of mixed ash stands (in southern Britain)

The main natural trends recorded in mixed ash stands in southern Britain on calcareous, base-rich, clayey brown earth soils at Monks Wood study site are given in Table 4.1. They indicate that ash should remain as a major tree, but with oak, field maple, hawthorn, hazel, and birch remaining as important long-term associates depending on the predominance of exclusion and browsing, incidence of wind damage and drought, and other factors.

Similar trends have been observed in other minimum-intervention reserves, most notably in maturing stands on calcareous soils at Lady Park Wood. Here, ash became the main tree species along with some standards of oak, growing over a mixed understorey of hazel with some field maple, hawthorn and various other species – birch had been prominent until it was set back by the 1976 drought – admittedly, the soils here are somewhat different than at Monks Wood, and beech and wych elm (which would have otherwise been locally prominent) have been set back here by grey squirrel debarking and Dutch elm disease (Peterken & Jones 1989, Mountford 1994, Mountford unpublished data).

Some aspects of the trends recorded at the study sites are also apparent more widely in other semi-natural lowland ashwoods in Britain. Rodwell (1991) writes that in general such woodland on base-rich soils frequently comprises mixtures of any persisting oak standards with much coppice regrowth and maiden ash, lesser amounts of coppice field maple (which grows less tall but is tolerant of shading by ash), and a persistent understorey of hazel (where the shade cast by trees is not too intense) and hawthorn sometimes with some blackthorn, dogwood, elder, spindle and/or other shrubs. Much the same is written by Rackham (2003) in reference to neglected coppice stands of this sort in ancient semi-natural woods in eastern England, though he also notes that often ash can overtop and kill the residual oak standards and that hazel can remain strong sixty years after abandonment (though the stools become much less vigorous).

Although the long-term fate of such woodland left to natural development remains open to some speculation and can be defined only in general terms, ash appears assured of remaining the dominant tree unless other, more shade-tolerant trees become invasive, notably suckering types of elm or possibly hornbeam or sycamore (Rackham 2003), though these shows no signs of vigorous expansion in Monks Wood at present (Steele 1973). Although ash is not an exceptionally long-lived tree, it has strong powers of

regeneration from seed and stump sprouts, even in relatively small gaps, and can therefore be expected to form a major part of the regeneration that develops as the canopy breaks-up. Although a severe windstorm might destroy large, even-aged patches of mature ash, it is likely that gap creation will be patchy and episodic, resulting in a degree of uneven-agedness. Some wind damaged ash may well develop in a pollard-like form into old age and, potentially, a scatter of very long-lived oak (and a few wild service) could join these. The very long-term position for oak is unclear, however, because of its recent difficulties in regenerating from seed, though this may change if large canopy gaps are created.

Field maple also appears capable of persisting for a long time as an associate to ash and, perhaps, even outlasting it and in places blocking subsequent regeneration. It is appeared somewhat but not exceptionally more vulnerable to drought than ash, but is unlikely to be as prolific as ash amongst seedling regeneration and may regenerate best by sprouting. On these grounds, it seems that field maple might be less important that at present. Opportunities for birch and aspen will be greatest if canopy break-up occurs sooner rather than later and (in the case of birch) there are no severe drought years. Provided a source of seed exists within a few hundred metres it is possible that birch will colonise gaps, though if these are only small then it is unlikely that birch recruits will make canopy trees.

Hawthorn and hazel seem quite capable of persisting right through the rotation of ash. They will benefit and develop as mature ash and field maple stands break-up, even if they suffer some damage from falling trees and branches. They may well block seedling regeneration of ash and other trees. Common hawthorn could form some long-lived trees, whilst hazel and midland hawthorn could persist as long or longer from stool sprouts. Nevertheless, hazel has proved less tolerant of overtopping, possibly suffered from drought, and its seed production is strongly hampered by shading and predation by grey squirrels. It will have to rely more on sprouting than hawthorn. Several others shrubs

appear capable of persisting below closed stands, albeit in lesser numbers and moreover where shading is least intense. Amongst these, blackthorn could develop in gaps into dense thickets blocking tree regeneration and forming self-perpetuating, long-lived thickets. Other species, however, look more likely to be only minor constituents of regeneration in gaps, particularly if the gaps are small and poorly-lit.

Thus, it seems possible that such woodland will generate mature mixed stands, mainly of ash with some field maple and a little oak, growing over an understorey of mainly hawthorn and hazel, and probably with some or many patches where the understorey is quite plentiful and perhaps including thickets of blackthorn. Future regeneration will rely on the effective control of deer. Assuming at least some browsing occurs, this could favour aspen, field maple, hawthorn and birch over ash, hazel and oak. The main agents of canopy disturbance should be windstorms and (for birch) drought. A scatter of long-lived, pollard-types trees could develop, some toppled trees could survive and much regeneration could come from sprout growth.

4.2.3.3. Natural development of mixed oak-lime stands (in southern Britain)

The main trends recorded in naturally developing mixed oak-lime stands in southern Britain on moderately acidic, base-poor stagnogley/brown earth soils at Langley Wood study site are given in Table 4.1. They emphasise the potentially dominant role that lime can have, though lime is often lacking in such stands leaving scope for oak, ash, birch, hazel, hawthorn and other species depending on the predominance of exclusion, browsing and squirrel debarking, incidence of drought and wind damage, and other factors.

Similar trends have been observed in other minimum-intervention reserves, most notably in maturing stands on moderately acidic soils at Lady Park Wood. Here, birch became widely abundant but was set back by the 1976 drought, oak remained locally dominant as a

retained standard tree, lime became locally dominant where it grew from groups of coppice stools, and hazel and some hawthorn and various other species persisted in places in the understorey – beech, which would have otherwise been locally prominent, was set back by grey squirrel debarking (Peterken & Jones 1989, Mountford 1994, Mountford unpublished data).

Similar trends are evident more widely in semi-natural lowland oakwoods in Britain (Rodwell 1991, Rackham 2003). Here, oak is the most common tree and quite often very abundant as a retained standard tree of derelict coppice woods. The commonest associate is birch, which can be very prominent in gaps and younger stands. Other trees are normally scarce, though on more fertile soils ash and some field maple and other species can occur. In certain woods, especially in the south-east, there are locally dominant populations of lime, hornbeam and sweet chestnut. These woods generally have a distinct and sometimes fairly dense understorey, especially on less acidic soils, depending on the degree of overstorey shading. Hazel is the commonest shrub and hawthorn the most common associate. In places holly can be quite common and occasionally there is some blackthorn and/or other shrub species present.

The long-term fate of such woodland left to natural development is open to some speculation and a variety of outcomes can be expected. Where lime is present it seems that it will become almost exclusively dominant, save for any well-established oak standards, which could persist for many centuries though any nearby lime growth is likely to exclude them by growing up around and even through them. Lime appears capable of living for many centuries and presumably extant lime coppice stools will thin down to a few dominant, long-lived stems. However, it is not clear how these will cope with windstorms when large, though any toppled or broken trees are very likely to redevelop from sprout growth. Lime might spread where branches or toppled stems layer around existing lime

stools and where seedlings develop, though cool summer temperatures could limit seed production and all low-growth is vulnerable to deer browsing. In addition, lime is unlikely to spread far and in many places quite different woodland can be expected.

Where beech, hornbeam, sycamore or sweet chestnut are present, these could also become locally dominant and spread into neighbouring stands. Beech and sycamore, being rather shade-tolerant, could develop below strongly birch-oak canopies, and hornbeam appears capable of establishing under the same conditions. However, beech and sycamore will very likely be hampered by grey squirrel debarking as they are very susceptible to this. The long-term relationships between these species and birch and oak in natural stands of this type could be usefully studied to see: (i) to what extent they can invade; and (ii) if chestnut is a replacement for hornbeam (and beech) and if all are replacements for lime, as is suggested from some ancient woods in south-east England (Rackham 2003).

In stands lacking these species, well-established oak standards appear capable of living for many centuries. They may well redevelop after wind damage in a pollard-like form and grow like this into old age. As in other woodland types, the very long-term position for oak is unclear because it has largely failed to regenerate from seed in recent times, though it may well develop if large canopy gaps are created. Birch is likely to persist between canopy oak for perhaps only a century or less before dying off due to old age, drought and/or wind damage, possibly very rapidly. It could replace itself if large, unvegetated gaps develop, but it could easily be replaced by ash or lime saplings, or by hazel or hawthorn bushes that have persisted in a suppressed state in the understorey, or even by persistent stands of bracken that have developed below the mature canopy of birch. The less seed-bearing birch trees that remain in a stand and the smaller the canopy gaps that develop, the less likelihood there is that birch will form an important part of any regeneration groups. Although ash is typically scarce in such woodland, in places it can form part of the canopy

and even seed into mature oak-birch stands lacking significant amounts of ash. Possibly it could benefit from an improvement in soil fertility associated with the presence of birch trees and following a reduction in nutrients caused by the repeated removal of underwood crops during coppicing (Rackham 1967). Provided there is a local source of seed-bearing trees, it can be expected that ash will develop even in relatively small canopy gaps where soil and light conditions permit adequate growth. However it is highly palatable to large herbivores. Ash are fairly long-lived and could easily outlast any associated birch.

It was shown at the study sites that hazel, hawthorn and, to a lesser extent, blackthorn, field maple, crab apple and yew individuals could persist in places in the understorey in such woodland, especially where not too heavily shaded. In addition, hazel, hawthorn, blackthorn and holly showed that they could invade below mature, part-broken birch-oak stands, though this was reliant on limited deer browsing. Once canopy gaps open further in such stands, notably as birch falls away and oak is wind damaged, these species would then be well placed to develop and block regeneration of trees. Common hawthorn, holly, field maple and yew could grow into large and long-lived medium-tall trees, whilst hazel and blackthorn could persist for many centuries by repeatedly sprouting or suckering. This is less likely to happen where the soils are more strongly acidic and infertile and overstorey shading has been severe, notably by oak and even more so by lime, hornbeam or sweet chestnut, though holly is more tolerant of both conditions. Hazel may also be hampered by predation of hazelnuts by grey squirrels, which could limit it chances of colonising gaps where it has previously been excluded.

Thus, the long-term fate of such woodland is highly dependent on whether stands contain lime or if beech, hornbeam, sycamore or sweet chestnut are allowed to invade to such areas. It seems likely that lime will to come to dominate any area it exists in, but spread only slowly from these. In birch-oak stands, oak could grow into a veteran tree, but birch

would be much shorter-lived and probably end up largely restricted to patches where there has been large-scale wind damage. Gaps, especially on more fertile soils, are likely to be filled or contain some hazel and hawthorn and other shrubs/medium trees, and ash might also invade in such situations. Assuming at least some browsing occurs, this could favour birch and hawthorn over ash, hazel, holly, lime and oak. The main agents of canopy disturbance will be windstorms and (for birch) drought. The stand structure is likely to be variable, depending on the species present and occurrence of disturbances. A scatter of long-lived, pollard-types trees could develop, some toppled trees could survive and a good deal of regeneration could develop from sprouts. If beech, hornbeam, sycamore or sweet chestnut invades, then these could become the long-term dominants and entirely change the stand dynamics. This has become much less likely as beech and sycamore are often the target of grey squirrel debarking.

4.2.3.4. Natural development of mixed oak stands (in north-west Britain)

The main trends recorded in naturally developing mixed oak stands in northern Britain on moderately acidic, base-poor stagnogley/brown earth soils at Clairinsh study site are given in Table 4.1. They indicate that oak should remain as a major tree, that holly and rowan should be prominent as the main species tolerant of shade, and that birch, hazel and some other species should remain important depending on the incidence of wind damage, predominance of exclusion and browsing, and other factors.

The trends can be compared to those recorded in minimum-intervention stands at Wistman's Wood (Proctor *et al.* 1980, Mountford *et al.* 2001a) and Black Tor Copse (Barkham 1978), though these occupy exposed locations in south-west England on the Dartmoor plateau, grow on infertile, acidic soils, and have a long history of wood pasturage. At both sites, oak has grown into the main canopy tree despite suffering some snow-breakage, and rowan is the main associate growing in sites protected from large

herbivores. Holly is rare at Wistman's Wood due to browsing, whilst birch and hazel are virtually absent. In addition, similar trends are evident more widely in semi-natural oakwoods in northern Britain (McVean & Ratcliffe 1962, Rodwell 1991). Mature stands here are generally overwhelmingly dominated by oak with birch often only a low-canopy cover component or a gap-coloniser. Rowan, holly and hazel are widespread and in ungrazed stands and can thicken up considerably, though hazel normally occurs only as a scattered bush beneath an oak canopy. Other trees and shrubs are usually scarce.

How such woodland will develop in the long-term left to natural development is again open to some speculation and a variety of outcomes can be envisaged. Windstorms are likely to be the main disturbance, but snow and ice-breakage may also be important as revealed by records from Wistman's Wood (Proctor *et al.* 1980, Mountford *et al.* 2001a). Although a severe windstorm might blow down groups or more extensive patches of mature oak and birch, it is likely that gap creation will be patchy and episodic, resulting in a progression of small-medium gaps with only occasional large blow downs.

Small gaps could easily be filled by crown expansion on bordering oaks, though suppressed birch appear capable of withstanding shading for some time and can recover once released. Nevertheless, birch is likely to decline where disturbance remains small-scale, even though individuals trees may well last longer than in more southerly situations where drought commoner. Small-scale gap creation in mature stands seems very likely to benefit the development of holly and rowan in the understorey, though this is dependant on low browsing pressure. Both are capable of growing into quite tall trees that could replace small groups of birch and oak lost from the canopy. In addition, holly is capable of developing into dense thickets that may well block subsequent regeneration of birch and oak. Alternatively, holly could play an important role protecting tree seedlings (particularly rowan and oak) from large herbivores, where browsing concentrates holly in patches and

stop trees regenerating outside its 'protective' cover (*sensu* Morgan 1987b). However, this seems unlikely to happen if herbivores are abundant.

Large-scale gap creation will favour regeneration of birch and oak from seed, expansion of suppressed hazel bushes and other light-demanding shrubs, and many standing or toppled oak trees may well regrow from sprouts. Indeed, well-established oak could potentially be very long-lived and recover from repeated wind and snow breakage in a pollard-like form. There is some question over the ability of oak and hazel to regenerate from seed, especially as grey squirrels have colonised many oakwoods in the north and west and could be a serious predator of their seeds.

Beech and sycamore could invade such woodland provided seed-bearing trees are present nearby. They are rather shade-tolerant and would be major competitors to oak and birch, changing the stand dynamics greatly. This is less likely where grey squirrels are present as they frequently target both species when debarking trees.

4.2.3.5. Natural development of wet woodland stands

The main trends recorded in naturally developing mixed stands on base-poor and moderately base-rich stagnogley and gley soils are given in Table 4.1. Such woodland was the most poorly represented type within the study transects, crossed only by small sections of the transects at Langley Wood and Clairinsh study sites. In addition, there are few other studies of how stands of this type of woodland will develop in the long-term. Nevertheless, the general features reported are evident more widely in semi-natural wet woodland stands around Britain (Rodwell 1991), i.e. grey willow is characteristically dominant on the margins of open water, whilst on less saturated soils further inland, stands are usually more mixed and alder, birch, ash and/or oak become increasingly important.

It was notable how grey willow dominated the stands that fringed the loch at Clairinsh. It seemed that, as alder, birch and oak were kept in check here by water logging, it could occupy such ground almost indefinitely by repeatedly layering and regrowing each time it was toppled as a mature bush. Once fallen, grey willow seemed to trap sediment and stabilise the ground for it to develop on. Perhaps, in time, it would thereby create conditions suitable for alder or other taller trees to colonise and replace it, though there were no signs of this happening. Rather, it seemed possible that such stands might be limited by severe windstorms that remove sediment and undermine established bushes. Nevertheless, somewhat inland there were more mixed stands with ash, alder, birch and various shrubs prominent. These remained relatively low growing, open and shrubby, with no large overstorey trees. It seemed like these would remain as such for many decades, with perhaps a tendency for shrubs, alder and birch to give way to ash and oak, though not everywhere. More observations are needed to clarify possible changes in this situation.

On even less saturated ground at Clairinsh, ash, alder, birch and oak grew into normal, tall overstorey trees. Over time there was a tendency for well-established oak to become dominant in the overstorey, for rowan and holly on base-poor soils to develop in the understorey, and (as recorded at Langley Wood) for ash to come in under birch. In another study of changes in wet woodland stands at The Otterskooi reserve, The Netherlands, Koop (1989) also found that there was a tendency for alder-birch stands to be replaced mainly by ash-oak stands with some rowan. Thus, such stands tend to act like equivalent dry woodland types, except for the prominence of species characteristic of the wet soils during the early stages of stand development. It is likely that any patches dominated by ash, alder and birch will persist for perhaps only a century or two given their potential lifespan. Oak, however, might dominate the overstorey for many centuries, especially if it can stay standing and shed branches during windstorms (and it might be more vulnerable to uprooting on such soils than normal). Ash, rowan and holly appear most capable of

developing in small gaps and also replacing any birch groups not excluded by oak. Alder groups might also be replaced in the same way by ash, if the pattern of replacement recorded by Tapper (1993, 1996) on a Swedish Island is repeated under British conditions. However, alder and birch might simply reoccupy patches they dominate, particularly if they collapse simultaneously and regrow from stump sprouts. This could equally apply to ash and oak. Large-scale gaps are also likely to afford opportunities for seedling regeneration of many species.

4.3. Major processes governing the long-term growth, mortality and regeneration of trees and shrubs in natural stands

This section deals with the next major part of the discussion and synthesis: the elucidation of the major processes governing natural stand development. The combined records of stand development from the study sites provided a wealth of information on this, though the degree of coverage varied from one aspect to another. In the following sections the major processes recorded/observed are described, discussed and compared to relevant literature.

4.3.1. Exclusion

Stem exclusion (*sensu* Oliver & Larson 1996) was a major factor affecting stand development at all of the study sites. It appeared to be the predominant process controlling growth and mortality and preventing recruitment where trees and shrubs formed a closed canopy. This process became predominant once individual stems were forced to compete with each other for growing space in the canopy. Some stems had apparently been given an early advantage, apparently because they established earlier or had been retained, were further from competitors, occupied more favourable growing sites, and/or suffered less from herbivory or other debilitating agents. As a result, these developed larger, more vigorous crowns, attained faster rates of growth, and grew taller and larger than less

vigorous neighbouring stems. Where stems were overtaken they became shaded, physically restricted, and starved of access to light and nutrients. Typically this caused the crown to lose vigour and die back, particularly if it was of a light-demanding species. As the crown and leaf area fell, so did the rate of stem growth, establishing a negative feedback whereby suppressed stems became ever more weakened until they were eventually excluded. Such individuals were also prone to damage by falling branches and trunks that fell from the overstorey.

The effects of exclusion were detected in all of the main stem populations, and especially those that developed into tall trees as even-aged cohorts in more or less closed stands (see Sections 3.1-6, 4.2.1.1-6). Within these there was a clear tendency for progressively smaller-sized stems to: (i) be less tall, leaning, overtopped and growing in lower canopy layers; and (ii) have smaller crowns, more frequent die back, slower breast height increment rates, and higher rates of mortality. The reverse applied to the larger stems in each population, though medium-tall tree and shrub species were not capable of growing into the upper canopy, so even the largest stems were only in the sub-canopy or understorey. Thus, initial size appeared to be a basic surrogate for the resource gathering potential of each stem, small stems having small crowns and (presumably) limited root systems.

Basal area increment rather than girth/diameter increment appeared to best represent growth rates in stem populations in closed stands undergoing exclusion (see sub-sections on the analysis of stem growth in Sections 3.1-6). The regressions of basal area increment on initial basal area size almost invariably accounted for a substantial part of the variation and showed that increasingly larger stems had higher increment rates. The same regressions based on girth/diameter values were often insignificant or demonstrated a weak positive trend, which sometimes plateaued or peaked amongst middle-sized stems. This

seemed to be because girth/diameter increment was dependent on stem size: a 1cm wide growth ring or girth increment represented a very different basal area increment on a tree with a small versus a large trunk. Thus, as stems became middle-large size increased it was only to be expected that girth/diameter increments would plateau/peak irrespective of them remaining vigorous.

Many studies have used girth/diameter increments as a measure of whole-stem growth and tree vigour (e.g. Lorimer 1981, Peterken & Jones 1987, Wyckoff & Clark 2002), whilst others have used basal area increment (e.g. Biondi 1996, 1999, Jaworski & Paluch 2002) or both (McDonald *et al.* 1996). However, in an examination of the relationship between long-term breast-height and whole-stem growth indices in overstorey red spruce trees in eastern North America, LeBlanc (1990) found that tree and stand maturation caused a long-term, progressive decline in annual ring width which did not reflect actual whole-stem growth performance (as expressed by the annual volume increment). Basal area increment was, however, strongly correlated to the annual volume increment, though it consistently overestimated the annual volume increment during the 30-50 years after release. Both of these measures showed a positive age-related increase for about 100 years after release, followed by an asymptotic level that was maintained for many decades. Phipps & Whitton (1988) detected a similar long-term basal area increment trend amongst white oak overstorey trees, and Pedersen (1998) found that the basal area increment of such trees could be reduced and sent into a terminal decline by environmental stresses, especially drought. White (1998) has identified three phases of basal area growth based on measurements of long-lived trees in Britain (including a formative period when basal area increment increases, a mature phase basal area increment plateaus, and senescent phase when basal area increment declines), and describes a method to use this to determine the age of veteran trees.

This study supports the use of basal area increment as a superior representation of whole-stem growth than ring width increment, as emphasised in the above studies and by Biondi (1999). It also detected a positive age-related increase in the basal area increment of beech and oak trees in each generation at Denny. This appeared to have increased up to at least 200-250 years in trees that survived to become canopy dominants and thereafter it declined, though the latter coincided with a period of drought that may well have significantly retarded growth. The records from Clairinsh also showed that the basal area increment of some mature oak trees here, which were probably about 200 years old, declined from 1961-86 to 1986-98 despite them retaining reasonably vigorous crowns.

Over time, the size-related patterns of growth, stratification, die back and mortality associated with exclusion generated right-skewed size-class distributions in most stem populations recorded at the study sites. These broadly comprised: (i) a few large, rapidly growing, 'winners'; (ii) a mass of medium-small, suppressed, 'second-place' stems with low-moderate mortality rates; and (iii) a minority of very small, strongly suppressed 'losers' with high mortality rates. The potential winners and losers could be recognised fairly early after canopy closure (see Figure 3.3.2). Windstorms, drought, grey squirrel debarking and other agents confounded this interpretation where they killed or damaged dominant stems or released hitherto suppressed stems. In addition, understorey shrubs (hawthorn, hazel, holly) tended to be slow growing and stem size measurements were often imprecise so breast height increment patterns tended to be highly variable.

The same patterns of size-related mortality, growth and population structure have been widely recorded in other closed stands during their development, e.g. the young-growth stands at Lady Park Wood reserve (Peterken & Jones 1987, Mountford 1994). They apply more generally to plant populations, with the mortality associated with this process being commonly known as 'self-thinning', 'regular mortality' or 'competition-induced death'

and the associated changes in population size structure having been described statistically by the –3/2 self-thinning rule (Yoda *et. al.* 1963, White & Harper 1970, Ford 1975, Mohler *et al.* 1978, White 1981, Peet & Christensen 1980, 1987, Oliver & Larson 1996). They represent a relatively predictable, autogenic pattern of development, determined mainly by the growth and influence of individual plants on each other, the inherent biological capacity of each species, and the performance of individual stems within each population.

Many trees produced a flush of epicormic sprouts on the upper trunk and/or crown branches in response to suppression and crown die back. Although this was not comprehensively recorded, it was observed on ash, beech, birch, hawthorn, lime, oak and yew. Presumably it was associated with a reduction in cambial activity and possibly changes in the hormonal balance (Oliver & Larson 1996, Nicolini *et al.* 2001). It helped by reinforcing the crown foliage and photosynthetic potential of suppressed trees, but appeared to do little to prevent long-term exclusion. However, the presence of epicormic shoots and buds gave stems an advantage when they were released into gaps (see below).

Exclusion was a gradual process: normally it did not create sizeable canopy gaps in young stands as the vacated growing space was quickly filled. Even where windstorms or other agents formed small gaps in the overstorey, surviving trees tended to fill these rapidly. It affected species that were more light-demanding and had a lower maximum height. The foliage of several species proved relatively intolerant to shading. Tall, light-demanding trees (birch, ash, oak) tended to sustain little or no foliage in the sub-canopy, especially if they were shaded from the side by densely crowned trees. Such high-crowned trees tended to have a light crown with low leaf area. They cast a light shade and allowed a degree of light to pass directly through. Shade-tolerant trees (beech, lime) tended to develop deeper, multi-layered, heavy crowns that cast a heavy shade and let little light through.

It was clearly important for strongly light-demanding trees to grow tall and sustain rapid growth if they were to avoid being excluded. Many species did not grow so tall: some developed only into sub-canopy trees (crab apple, field maple, goat willow, rowan, wild service, yew); many almost reached the sub-canopy (e.g. blackthorn, elder, hawthorn, hazel, holly); and some formed only short understorey bushes (e.g. broom, guelder rose, privet). Many shorter individuals struggled below the shade of heavy crowned trees, but a few proved more shade-tolerant (hawthorn, hazel, holly, field maple, rowan, wild service, yew), especially where the overstorey was composed of light crowned trees.

Thus, exclusion had particularly severe effects where shade-tolerant trees were abundant. Such trees caused a strong decline in light-demanding species due to exclusion, so species richness tended to show a marked decline over time, especially in the substratum, but also in the overstorey. In woods dominated by more light-demanding trees this trend was much less pronounced and species richness tended to remain reasonably high. Below a light canopy of ash at Monks Wood it seemed that most species present within the stands had managed to persist for many decades, albeit that the abundance of some had probably declined markedly, whereas in beech stands at The Mens saplings of more light-demanding species were soon excluded once gaps closed. In addition, the substratum at Monks Wood remained generally well developed, whereas at The Mens it was much more restricted.

4.3.2. Wind damage

4.3.2.1. Damaged caused

Strong winds damaged overstorey trees at all of the study sites. This included: (i) snapping of branches or boughs or much of the crown; (ii) snapping of the trunk either low down or higher up; and (iii) uprooting or partially tipping of whole trees. Smaller overstorey trees tended to suffer such damage when large neighbouring trees fell onto them. Wind damage proved to be a major cause of mortality and crown reduction for dominant overstorey trees,

though by no means did all wind damaged trees die. Most of the major canopy species that formed large trees were affected. At Denny and The Mens a good many beech and some oak were toppled or snapped. At Toy's Hill most of the mature beech present and the few oak were brought down or snapped in the 1987 storm. At Clairinsh, a few large oak, birch and ash were uprooted, snapped or part-tipped, and many surviving oak had broke branches out. At Langley Wood, several large oak had crown branches snapped out and a good number of birch were brought down. At Monks Wood, a few canopy ash and field maple were snapped or uprooted.

Various factors made individual trees more prone to wind damage. Position in the overstorey and large crown-size proved generally important in determining if trees were directly damaged. Beech and birch proved vulnerable to uprooting as they were superficially rooted, whereas oak proved more wind-firm but tended to snap off and shed crown branches. Tall, slender trees and particularly outgrown beech pollards also appeared vulnerable to uprooting or breakage, as were trees exposed in or beside pre-existing gaps, trees that were growing on a lean, trees that had long projecting branches, and stems that were poorly attached. Those that were prevalent as subordinate overstorey and sub-canopy trees proved vulnerable to indirect damage, especially from large falling trees.

Some overstorey trees died as a result of wind damage, but in various cases the effects were sub-lethal and sometimes individuals made a substantial recovery. A good many standing wind-snapped and one uprooted oak recovered especially by sprouting. The tendency for oak to snap and recover by sprouting made it particularly resilient to wind damage. However, badly broken and toppled oak often ended up overtopped and growing slowly in the substratum: most uprooted trees were subsequently excluded. Some broken beech also made a strong recovery and, in addition, several uprooted beech remained alive on the ground in a reasonable state, though these struggled on dry sites and did not look

like shooting up into replacement canopy trees. It has been suggested that horizontal living trees might have been common in the original-natural woodland of Britain (Rackham 2003). The evidence suggests that some may well have been present, particularly in large gaps and of more shade-tolerant species elsewhere. Probably much more common were snapped and part-broken oak and other trees growing in a pollard-like form.

Falling branches and trunks from wind damaged overstorey trees inevitably crushed, broke and toppled individuals that lay in their path in the substratum. This included invading and suppressed individuals, especially of beech, hawthorn, hazel, holly and rowan. Some of these died (or at least the stem concerned did), some survived but were left slow growing, whilst others recovered well by resprouting. This depended on the degree of damage, the extent to which the canopy was opened afterwards, the shade-tolerance of the species concerned, and the tendency to produce sprouts. Sprouting was observed on a wide-range of species and in some cases such sprouts grew strongly and helped or were paramount in the recovery of the damaged individual. In addition, some individuals that ended up prostrate or pinned to the ground rooted into the soil at the point of contact, i.e. they layered. This was particularly noticeable in hazel, hawthorn and holly, but occurred in other species. Most native trees and shrubs readily sprout after being broken (including breakage caused by coppicing or pollarding), though certain species sprout more strongly from the base than high up. In fact, sprouting is a widespread phenomenon in angiosperm trees and shrubs (Everham & Brokaw 1996, Del Tredici 2001). This is clearly an important attribute for understorey individuals as the likelihood of being hit and damaged is reasonably high. The ability to layer can be an effective mechanism to take advantage of such 'damage' and for individuals to spread.

4.3.2.2. Wind damage as an agent in gap formation

Wind damage affected large overstorey trees and produced canopy gaps at all the study sites. It was associated with autumn/winter gales and occasional severe hurricane-type storms, as in 1987 when wind speeds temporarily gusted to around 150km per hour across south-east England (Burt & Mansfield 1988).

Wind damage at most of the study sites was chronic and relatively small-scale, acting as a minor rather than a stand-destroying disturbance. Even worse windstorms left mainly small, scattered narrow gaps. At Clairinsh, the 1968 storm blew over a scatter of trees and broke branches/part-tipped some others that remained standing. Further small-scale wind damage occurred through to 1998. This opened a scatter of relatively small, narrow gaps up to c.10-100m^2. At Denny only a few trees appeared to have been blown down by the 1987 storm, but several were toppled in the 1990 storms and others had been irregularly toppled or broken during or before 1956-96. At Langley the 1987 storm broke a scatter of large crown branches and toppled a few other canopy trees. This mainly left small, narrow gaps. However, some larger gaps up to c.100m^2 developed due to more extended wind damage in certain places during or before 1986-96. At Monks Wood, a few canopy trees were wind-snapped during or before 1985-96.

At The Mens, the 1987 windstorm brought down a minority of the stands growing on steep slopes to the south of the reserve, but damage across most of the reserve was scattered and patchy and formed mainly small or occasionally medium-sized gaps (see Whitbread *et al.* 1993, Whitbread & Montgomery 1994). This was recorded in detail in the main study area where nine moderately clumped gaps of 463m^2 average area and covering 2.5% of study area were created when a number of beech and oak were toppled or broken (see Figure 3.2.1). Even where the canopy remained more or less closed, branches were wind-snapped from canopy trees leaving a scatter of debris and crushed understorey. This must have

thinned the canopy and created many more rather small openings. Thus, the gap size-distribution (see Table 3.2.18) formed an approximate negative exponential curve with three distinct size-groupings: (i) larger gaps, c.1000m^2 in area, including two of the gaps measured – these were created where groups of about 9-13 principle canopy trees were toppled by storm winds and the same number of secondary trees that lay in their path were broken/ crushed – they covered c.1% of the study area; (ii) small gaps, ranging from c.100-500m^2 in area, including seven of the gaps – these were created where small groups of canopy trees/crowns were lost and also covered c.1% of the study area; and (iii) very small gaps, formed by the small-scale localised breakage of boughs/branches from canopy trees – these were not easily definable from below and were not counted or measured as 'gaps' proper. The shape of the nine gaps that were measured was irregular but most tended towards oblong or circular. Nearly all non-circular gaps had the longest axis pointing towards ENE or NNE. These patterns reflected: (i) the position of large canopy beech and oak within the stand; (ii) the regularity with which large windblown trees brought down lines of other canopy trees in their path; (iii) the direction of tree fall as determined by the direction of the strongest gusts during the storm; and (iv) the quasi-circular canopy space occupied by canopy trees involved with gap creation. Similar, but less extensive, damage was recorded during 1988-98, most of which was put down to the storms of 1990.

A similar pattern of gaps as recorded at The Mens was created in 1987 at the nearby beech-oak stands at Ebernoe Common, and various observers reported the same general pattern of damage more widely (Whitbread 1988, 1991, Allen 1992, Peterken 1996, Rackham 2003). Most semi-natural woods in south-east England lost some canopy trees in the 1987 storm. Many had only a few or several patches blown down; large windblown trees frequently brought down other trees in their path (the 'domino-effect'). Some woods had localised swathes of severe damage, but only a very few suffered catastrophic blow down across many hectares. As most of the trees fell towards N-NE-E (see Cutler *et al.* 1990, Allen

1992), presumably many of the gaps created elsewhere were similar in shape/alignment to those at The Mens.

Several near-natural reserves in continental north-west Europe have sustained similar damage during severe windstorms. In a detailed study of mature beech-ash stands at Suserup Skov reserve (Denmark) (Bigler 2002a, Emborg *et al.* 2002), a severe windstorm in 1999 increased the gap cover from 8-14%. Although two gaps were sized 4250-4375m^2 these were on sites with a high water table. The other gaps included four of 1000-1500m^2, eleven of 500-850m^2, but most were <400m^2 and the average was only 450m^2. Most toppled trees were left lying towards NE, many large windblown trees brought down smaller trees, and most gaps notably narrower than wide. Similar studies at Draved Skov reserve (Denmark) (Bigler 2002b, Wolf & Bradshaw 2002, Wolf *et al.* 2004), found the same windstorm uprooted/broke about 4% of trees in mature beech-oak-alder-lime stands, creating gaps of 25-300m^2 area in one compartment and 25-2500m^2 in another. Most trees fell towards the east, with a high proportion of the multi-tree gaps being produced by one tree falling on another. Windstorms in 1967 and 1990 at Fontainebleau created a range of small to large gaps and most trees falling E or NE. This left 7.5-8% gap cover at La Tillaie reserve, but at Le Gros Fouteau reserve the 1990 storm did much more damage (4.5% versus 20.5% opened) (Pontailler *et al.* 1997). Rather similar patterns of wind damage are also recorded for old-growth woodland in eastern North America (Runkle 1982, 1990, Tyrrell & Crow 1994).

The exception to this pattern of small-scale damage was Toy's Hill, where most of the old beech stand across 50ha was lost. This was far greater than compared to even the 1990 blow down at Le Gros Fouteau. Some other sites in southern England also suffered severe blow downs in 1987, including several parts of the East Hampshire Hangers where patches of mature beech growing on steep, chalk scarp slopes with shallow-soils were extensively

damaged (Mountford 2004, Mountford & Ball 2004). The view was that the 1987 windstorm was especially damaging because the trees were still in leaf and the soils had been saturated by heavy rainfall beforehand (Whitbread 1991).

The patchiness of damage observed in the 1987 windstorm across south-east England was explained by a range of factors (Whitbread 1988, 1991, Peterken 1996): (i) the most destructive winds were to the south and east of the storm centre; (ii) the storm generated short, unpredictable, severe internal gusts, with multiple, parallel, turbulent wind-lines evident; (iii) the land configuration protected some sites (south-facing slopes and scarps were affected widely, whilst north-facing slopes suffered less) – however, some sites suffered from lee-slope turbulence or from funnelling and wind constriction along (narrow) north-south valleys and towards the top/along steep slopes (e.g. Mountford 2004, Mountford & Ball 2004); (iv) mature stands on soils that permitted only shallow or infirm rooting (notably on chalk slopes, stagnogleys, sands and gravels) were particularly vulnerable to uprooting; (v) large, maturing, tall, slender, and multi-stemmed trees with signs of stem or root decay generally proved more vulnerable to windstorm damage; and (vi) certain superficially rooted species (beech, birch) proved susceptible to uprooting, whilst others characteristically suffered from trunk breakage (hornbeam, field maple, ash) or crown shredding (oak); and (vii) the regularity with which large trees brought down other in their path.

Several of these factors proved important at The Mens. It certainly lay in the path of the most destructive winds. Lee-slope turbulence was blamed for the windblown block of mature beech-dominated woodland to the south of reserve growing on steep, north-facing slopes (Whitbread 1988). However, across much of the reserve the relatively deep, clayey soils proved wind-firm, with sporadic severe gusts best explaining the scattered pattern of

gaps. In the study area, the trees that were damaged directly by the storm were all large canopy trees and more beech than oak.

Some of these factors also help explain why damage was so severe at Toy's Hill. Firstly, the site was exposed on the highest plateau in Kent and lay in the path of the most destructive part of the storm. And secondly, the stand was dominated by outgrown beech pollards, which were only superficially rooted and had several large, long secondary trunks that were firmly attached to short boles and which evidently acted like long levers, enough to cause the whole tree to uproot (see Allen 1992).

The episodic pattern of wind damage recorded at Denny and Clairinsh and inferred from The Mens, Langley Wood and Monks Wood, suggests that mature stands will normally be affected by occasional winter gales every few years and notable windstorm damage only every few decades. This broadly agrees with records from other woodland reserves: Dendles Wood suffered notable damage in 1967-75, the early 1980s, and 1990 (Mountford *et al.* 2001b); Fontainebleau in 1967, 1990 and 1999 (Koop & Hilgen 1987, Pontailler *et al.* 1997, Wijdeven 2003a); Ridge Hanger and Noar Hill Hanger in 1974, 1987 and 1990 (Mountford 2004, Mountford & Ball 2004); Suserup Skov in 1967 and 1999 (Emborg *et al.* 1996, 2002); and Zoniënwoud reserve (Belgium) in 1990 and 1999 (De Keersmaeker *et al.* 2002). Lady Park Wood has suffered chronic wind damage throughout its recording history from 1945-2002 (Peterken & Mountford 1995, Mountford unpublished data).

Most of Britain, and the coastlands from northern France to Denmark share a similar wind regime, with the coastal regions and the northern and western parts of Britain being most windy (Quine *et al.* 1995). For Britain as a whole during 1961-90, 21 windstorms caused damage to forests or trees and an average of 12 severe gales were recorded per year (Broadmeadow 2002), though only 9 of 35 deep depressions that passed over Britain in a

recent decade went over southern Britain (Allen 1992). Historic records of past-major windstorms in Britain suggest that a wood can expect a devastating windstorm at least once in a century (Rackham 2003), though away from the coastal windbelts and higher hills this is increased to roughly every 200-300 years (Peterken 1996). The estimated return period for extreme windstorms (as in October 1987) is less than 50 years in north and west England, but is over 200 years in the south-east (Burt & Mansfield 1988, Hopkins 1994). A similar wind regime affects woodland in eastern North America, with the hurricane return frequency in New England ranging from 85-150 years at the coast at Boston to over 380 years in the interior mountains (Lorimer & White 2003).

4.3.2.3. Conclusions about wind damage

Wind damage is a major factor affecting the development of natural woodland in Britain. It can kill or damage overstorey trees, which in turn causes a good deal of damage to smaller individuals growing below. Windstorms act widely and occur regularly. Every year or few years damaging gales test the strength of the trees in a stand and cause minor damage or the occasional tree fall. This chronic damage is interspersed by more severe windstorms, which are much less common but can cause devastating blow downs in a few places, create medium-large gaps in other stands, and widely knock out individual trees and crown branches. Although the severity of damage is related to the vulnerability of certain sites and trees, it has much to do with the track of particularly storms and the internal patchiness of severe gusts. As the devastation at Toy's Hill clearly demonstrates, such rare, extreme, short-term events can utterly change the condition of a stand.

4.3.3. Drought damage

4.3.3.1. Damaged caused

Drought damaged trees at some of the study sites. It was mainly associated with the hot dry summers stretching over 1975 and 1976, when rainfall was only 50-70% of the long-term

average across much of south England (Doornkamp & Gregory 1980). In addition, the lesser drought years of 1983-84 and 1989-90 also affected trees. Drought damage was not recorded and did not have an obvious major impact at Clairinsh, The Mens, Toy's Hill or Langley, though it was suspected that birch might have been debilitated at the last two sites. Worst affected were large old beech and a few large oak at Denny Inclosure, which presumably had a large water demand. Drought also killed off maturing birch at Monks Wood, and possibly it caused a few large field maple and old hazel stools to decline here. It had no obvious affect on other species here, notably ash or oak. Both beech and birch proved vulnerable as shallow rooted species. In addition, they were growing on stagnogley-type soils, which restricted there root development and dried excessively, exacerbating the effects of drought.

Drought had a range of effects on trees: (i) sometimes it caused immediate death; (ii) sometimes a more drawn out death (notably in oak); (iii) sometimes it left trees alive but with parts of the crown destroyed or in a poor state and even with patches of dead bark up the trunk; and (iv) sometimes it caused crown die back and slowed the growth of trees that then recovered. Beech and oak trees that took some time to die often succumbed to disorders to they were normally resistant, drought having lowered their defences. This type of mortality spiral, where trees are weakened by a series of factors and eventually end up dying, is widely recognised as a major process in the death of trees in temperate woodland (e.g. Thomas *et al.* 2002).

Drought victims died standing and collapsed as snags, but were sometimes toppled by the wind. They did not normally break other trees, but occasionally they did crush individuals in the understorey.

4.3.3.2. Drought as an agent in gap formation

Drought mainly created canopy gaps at Denny Inclosure and Monks Wood. At Denny, these tended to open progressively over the next decade or so and of the 30% gaps covering the study transect in 1996 (see Figure 3.1.6) an estimated about 70-85% were due to drought-induced mortality and die back. Several of the individual gaps created were rather small or narrow and included areas of only c.10-200m^2. However, in places where drought had killed off groups of about twenty old beech they extended further, with up to c.800m^2 area within the transect and perhaps as much outside. The general decline in crown condition associated with drought must have lightened the canopy widely, but as many trees recovered from minor drought die back many small gaps must have quickly re-closed. The gaps created at Monks Wood by the 1976 drought were only small and localised as birch was only a minor canopy species. They had largely been filled by 1996. This pattern of drought damage to beech and birch was repeated in the unenclosed part of Denny (Mountford & Peterken 2003), in other New Forest woods (Tubbs 2001), Lady Park Wood reserve (Peterken & Mountford 1996), and there was widespread deterioration of mature beech trees reported across southern England (e.g. Lonsdale *et al.* 1989). It also affected beech in Germany (Asthalter & Lehmann 1979). The periodic sudden decline of oak reported across lowland England and central Europe during the last century is considered to be linked to a series of factors including severe drought (Gibbs & Greig 1997, Thomas *et al.* 2002). Drought also occasionally kills trees and creates gaps in woodland in eastern North America. Again, certain species and sites are more vulnerable, gap creation tends to be patchy and drawn out, and individual gaps are typically in the small-medium (40-850m^2) range (Hursh & Haasis 1931, Clinton & Boring 1993).

Drought is more frequent in southern than northern England with notable droughts recorded in 1934, 1947, 1955, 1975/76, 1984 and 1990, though the double drought years in the 1970s seemed to have a particularly damaging effect, possibly the worst for three

centuries. However, due to differences in the soil water regime, drought effects tend to be felt most on dry, shallow free-draining and stagnogley soils, upper slopes and raised ground, and southerly-facing slopes (Peterken 1996).

The above suggests that although droughts occur on average about once a decade and can cause widespread debilitation in certain stands, those that produce widespread mortality are much less frequent and depend on the species composition and maturity of stands and the characteristics of the underlying soils. Nevertheless, in certain situations severe drought can cause profound changes in stands.

4.3.4. Damage by large herbivores

At two of the study sites large herbivores had a dramatic impact on small trees and shrubs by browsing available foliage and debarking stems and larger trunks. At Denny, where deer and ponies increased to high populations, they stopped holly spreading and trees regenerating, and went onto destroy much of the understorey layer, including some large tree-like holly that they killed by debarking the trunk. Such damage can be observed widely across the New Forest, though damage it has been particularly severe at Denny. At Monks Wood, muntjac deer increased similarly and ate their way through much of the ash and other regeneration that had or was developing. They also killed off or checked small stems on hazel and other shrubs by browsing and debarking. Deer also had a significant impact on tree regeneration and shrub growth at The Mens, in particular by checking ash seedlings. However, they much less numerous here and accordingly did less damage and were more selective. Deer had only a limited impact at Langley and Toy's Hill, and there was no sign of deer damage on the island of Clairinsh.

Several species of deer are widespread within British woodland and have increased significantly in numbers in recent years (Corbet & Harris 1991). Livestock may also be

present either formally as a wood-pasture treatment or informally when fencing fails, and wild boar seem also to be on the increase. It is widely recognised that when large herbivores are numerous they can cause massive damage to low woody growth and prevent regeneration even in canopy gaps. Even when less numerous they can have a significant but more selective impact, related to their food preferences, composition and vigour of the vegetation, presence of protective features and other factors (Gill 1992, Putman 1994a 1994b, 1996, Putman & Moore 1998, Vera 2000, Gill & Beardall 2001, Kirby 2001, Rackham 2003).

Morgan (1987b) proposed that tree regeneration in the New Forest would be continuous with recruits growing up in holly that would be relatively immune to changes to the browsing regime. More recently, Vera (2000) has postulated that in the original-natural mixed deciduous woodland of Britain large herbivores were numerous in a grazed park-like landscape, yet all tree species and hazel were able to regenerate and grow into groves in the protection of thorny bushes. There was some evidence from The Mens that holly and fallen wood could play a protective role for tree seedlings, but only because herbivores were scarce and being selective. However, this was certainly not the case at Denny where herbivores were numerous: they destroyed much of the holly understorey that had developed and stopped almost all regeneration. Only the top of root plates provided effective protection for a few birch seedlings to recruit. It is difficult to see how palatable tree species and hazel could realistically sustain themselves under such conditions.

4.3.5. Damage by grey squirrels

Grey squirrels had an important impact on stand development at Denny, The Mens and Langley Wood by debarking trees. They mainly did this to beech and especially fast-growing, pole-sized beech released into gaps. This left most beech at these sites with patches of bark missing. Moreover, several large trees had major branches snap out,

several pole-beech were killed, and many more pole-beech were left with dead crowns, snapped tops and/or extensive wounds. In places this opened gaps in the canopy. It seemed unlikely that surviving debarked beech would last as long as their predecessors or that pole-beech would develop into replacement canopy trees. Severe debarking was also recorded on sycamore at Langley Wood and some birch poles at Toy's Hill.

The incidence of squirrel debarking increased greatly at the study sites from the 1970/80s and looked set to continue. It has become a widespread feature in British woodland and can clearly have a major impact on stand development, particularly in woods where pole beech are released into gaps. Grey squirrels do not debark trees to the same extent where they are native, possibly because they are less abundant due to predation (Kenward *et al.* 1988a). It is alarming that they have recently established wild populations and potentially could spread widely on mainland Europe (Bertolino & Genovesi 2002).

4.3.6. Disease and disorders

There were no major disease outbreaks recorded at the study sites, at least not isolated from the impact of drought, which rendered beech and oak trees at Denny and possibly hazel at Monks Wood open to fungal attack and other disorders. No doubt the position would have been different if elm had been part of the stand mixture, mature trees of which have been affected widely by the Dutch elm disease epidemic that started in the 1970s (see Peterken & Mountford 1998, Rackham 2003). At present this is the only stand destroying disease known in Britain. It is also epidemic in mainland Europe and North America.

4.3.7. Senescence

There was only limited evidence of individuals dying simply due to senescence in old age, at least judging by the crown condition of some of the oldest recorded specimens of beech, oak, ash, alder, birch, field maple, common hawthorn, holly and rowan. However, many of

these trees were well below their expected lifespan. Moreover, it was difficult to separate out deterioration or collapse due to old age from that associated with exclusion or drought or windthrow. For example, Denny contained a good number of mature beech and oak, which were three or even four centuries old. Although some remained healthy enough, several succumbed to the 1976 drought and these might have started to decline beforehand due to old age. In the same way, although some birch at Monks Wood, Langley and Clairinsh remained healthy after 60-100 years, many had already died due to drought, wind damage or exclusion. There were signs that old hazel stems and stumps had become senescent and died at Monks Wood, though again this was confounded by shading and possibly by drought and fungal attack. Whatever, it was apparent that certain species were likely to be relatively short-lived (notably birch, alder, aspen, rowan), whilst others had an intermediate longevity (ash, field maple, common hawthorn, hazel as a stool), or were potentially longer-lived (beech, oak, lime, holly).

A comparison of the potential lifespan of the species and their shade-tolerance (Table 4.2) showed that, regardless of their growth form, there was distinct tendency for short-lived types and to be relatively light-demanding, whereas longer-lived types had greater shade-tolerance. The notable exception was oak that was both a light-demanding tree and potentially very long-lived. These tendencies are also evident amongst the native trees and shrubs of eastern North America (Table 9.1 in Burrows 1990). The shortest-lived trees include birch, alder and aspen (with ash somewhat longer-lived) that tend to act as fast-growing pioneers early in stand development in large gaps created by major disturbances. Where these die away in mixed stands they tend to be replaced by slower-growing but longer-lived trees notably lime and/or beech, assuming these are present. If oak can get firmly established in young stands, it can persist right to the end of the development of a stand, or even several rotations of short-lived trees. Species that usually grow less tall include hazel, rowan, field maple, hawthorn and holly, all of which have a degree of shade-

tolerance. They can persist or invade to a greater or lesser extent below stands of pioneer trees and oak: holly can even do this below where understorey shading is more extreme below beech. This gives them an opportunity to expand as the canopy opens and block tree regeneration.

Table 4.2: Comparison of the potential lifespan, shade-tolerance and growth form of major species recorded at the six study sites. Based on material in **Section 4.2.2**

Species	Lifespan	Shade-tolerance	Growth form
Aspen	Short	Low	Tall tree
Birch	Short	Low	Tall tree
Alder	Short	Low	Tall tree
Hazel	Stems short, stool longer	Low-intermediate	Shrub
Rowan	Intermediate-short	Intermediate-high	Medium-tall tree
Field maple	Intermediate-long	Intermediate	Medium-tall tree
Hawthorn	Intermediate-long	Intermediate	Shrub/medium-tall tree
Ash	Intermediate-long	Intermediate	Tall tree
Holly	Long	High	Shrub/medium-tall tree
Beech	Long	High	Tall tree
Small-leaved lime	Long, stool very long	High	Tall tree
Oak	Very long	Low	Tall tree

4.3.8. Regeneration and release below gaps

4.3.8.1. Regeneration and release below part-broken canopies

Regeneration was strongly suppressed after canopy closure because established trees intercepted most photosynthetically active radiation and competition for soil moisture was presumably intense. However, as the stands aged and the base of the overstorey rose, small breaks started to arise due to minor disturbances and as overstorey trees occupied growing space less aggressively. This increased light and improved other conditions in the understorey (see Oliver & Larson 1996) and created growing space in the overstorey.

Accordingly, a low stratum of shade-tolerant shrubs and tree seedlings invaded below the stands and long-suppressed trees and shrubs were released and grew on. Obviously, the effect was most pronounced where more substantial and prolonged gaps were created and the canopy was composed mainly of light crowned trees. Invasion of the understorey was

particularly apparent with holly, which spread as a patchy, but pronounced low scrub by low layering/sucker growth at Denny, Clairinsh and The Mens. It also started to seed in at Langley Wood. Rowan also seeded in with holly at Clairinsh, and a few beech seedlings developed with holly at Denny and The Mens. At Langley Wood, several small hazel, hawthorn, holly, blackthorn, ash and hornbeam developed below birch-oak stands, and a mass of ash seedlings may have invaded below the area of wet birch stands. At Monks Wood, numerous ash seedlings and saplings developed along with some blackthorn suckers/seedlings and individuals of other species. Release of individuals was observed particularly in holly, rowan, hazel, hawthorn, beech and ash, but was a general phenomenon. Often they responded to quite small gap formation, as most individuals were of more shade-tolerant species.

Depending on the species, release was evidenced by an increase in the condition and vigour of the crown, the growth rate of extant stems, and by the development of additional trunk or basal sprouts. Sometimes a corresponding increase in the breast height increment rate was detected. Saplings and poles of tree-forming species like ash and rowan tended to respond by accelerating upwards with the leading shoot to get into the overstorey. More shade-tolerant beech trees tended to grow up as much they expanded their crowns, whilst holly did the reverse. Hawthorn tended to expand its crowns and develop from trunk sprouts, whereas hazel tended to mainly produce vigorous basal and trunk spouts.

Emborg (1995) identified the same 'rush' strategy of ash and slower 'stop-go' strategy of beech in response to episodes of release and suppression during stand development. He related this to the strategy of ash as a 'light-demanding (and short-lived) gap specialist' and to beech as a 'shade-tolerant climax species'. The response of birch and rowan also fits with them being relatively short-lived, light-demanding trees and their need to get into the overstorey whenever possible. The response of the other species fits with the relatively

short lifespan of individual hazel stems and the greater longevity of holly and (common) hawthorn. In eastern North America, Canham (1985, 1990) showed that the stop-go strategy applied to American beech and sugar maple, which could also withstand periods of prolonged suppression and exploit relatively short-lived canopy gaps that were typical of natural woods there.

4.3.8.2. Regeneration and release within larger canopy gaps

Larger canopy gaps were created at three of the study sites and these became a focus for tree and shrub regeneration, regrowth of damaged individuals, and release of hitherto suppressed individuals in the substratum and overstorey trees.

4.3.8.2.1. Regeneration and release within large gaps at The Mens

Where the 1987 windstorm created sizeable gaps in the canopy at The Mens the amount of light reaching the ground and understorey was increased. This encouraged understorey shrubs, tree regeneration and ground vegetation to grow, particularly in larger gaps. Most notable was the accelerated development of holly that started to develop in the understorey beforehand. In addition, suppressed and damaged bushes of hazel, hawthorn, crab apple and yew were released. In some places patches of ground vegetation developed, a few light-demanding shrub species recruited, and seedlings of mainly ash, beech and birch established, though only some developed into more vigorous saplings. Even so, some birch and ash did grow into vigorous poles or more slow growing saplings, and numerous beech established as stout, slow growing seedlings. The prospect for these to grow into tall trees was improved by the relatively slow-closure of gaps and subsequent fall and breakage of some border-trees. However, it seemed likely that in smaller gaps it would be mainly beech that continued to develop slowly upwards and survive periods of suppression.

The patchiness of the ground vegetation, general scarcity of tree regeneration and light-demanding shrubs, and slow-growth of tree regeneration was attributed to several factors. Most gaps were small, some had closed significantly within a decade, and many were narrow and aligned approximately SW-NE. Thus, the increase in illumination within gaps was limited and increased most in the centre and northern quadrant of larger, more circular gaps (Collins & Pickett 1987, Canham *et al.* 1990). Shrub growth, particularly holly, was vigorous and in other places dense patches of ground vegetation established: both would have acted as a general competitive barrier for tree seedlings. Seed sources for light-demanding tree and shrubs were generally scarce and distant, relying on the wind and animals to disperse it into gaps. Seed dispersal into gaps appeared to have been limited for beech, and seed production of beech and oak was probably irregular and suffered heavy predation. There appeared to have been little advance regeneration of beech or ash before the gaps were created and most surviving pre-gap beech saplings were damaged by storm debris or damaged by squirrel debarking afterwards. Deer browsing and bank vole debarking checked the development of tree seedlings, particularly ash. Soil disturbance was limited to a few upturned root plates and this could have particularly hindered birch.

4.3.8.2.2. Regeneration and release within large gaps at Toy's Hill

The 1987 windstorm open most of the stand at Toy's Hill and encouraged the ground vegetation and regeneration to develop strongly. Initially there was temporary surge in rosebay willowherb and foxglove, which characteristically invade bare, well-lit, acidic soils from wind-dispersed seed (rosebay willowherb) or seed that has lain dormant in the soil (foxglove) (Grime *et al.* 1988). Dense regeneration of birch or patches of bramble or bracken replaced these early colonisers within a few years. Where bramble spread areas over areas covered by crown debris, which birch did not colonise, it remained vigorous even eleven years after the storm and seemed semi-permanent. This happened in other in windstorm damage woods (Mountford & Ball 2004). Nevertheless, birch thickets ended up

covering much of the ground having probably colonised from seed trees at some distance from the study plot. Their distribution appeared to have been dictated mainly by the location of fallen trunks, crown debris, fallen live crowns, holly thickets and patches of bracken: they developed mainly outside of such ground. Recruitment of other species was scarce, though several holly developed/regrew particularly from low-growing bushes present beforehand. In addition, several crushed/snapped small beech were sprouting, a crushed rowan had sprouted strongly, and a large uprooted oak had developed some vigorous basal/trunk sprouts.

The scarcity of regeneration other than birch and holly was attributed to several factors. Few species other than beech and oak were present as seed-bearing trees in the original stand, so there was considerable reliance on seed dispersal by the wind or animals. Even beech and oak seemed to have produced little seed and/or suffered heavy predation, and deer browsing checked the development of at least some seedlings of species that did manage to establish. In addition, there appeared to have been little advance regeneration beech present beforehand.

4.3.8.2.3. Regeneration and release within large gaps at Denny Inclosure

Instead of tree and shrub regeneration developing below the extensive canopy gaps that developed at Denny, the main feature was the spread of patches of coarse grassland and bracken. There was little doubt that deer/pony grazing had blocked regeneration, however the ground vegetation may have played a significant part in preventing seedlings getting established. Much the same happened in the unenclosed part of Denny, though the grassland that developed here had a short sward tightly grazed by ponies (Mountford & Peterken 2003), indicating that deer browsing was the main form of herbivory inside.

4.3.8.2.4. Conclusions about regeneration within large gaps

The vegetation that developed in larger canopy gaps showed some general features. In particular, they were a focus for tree regeneration, growth of hitherto suppressed individuals, and expansion of the ground vegetation. Unlike in small gaps, they were places where light-demanding species could effectively recruit and grow rapidly. Developments within and between large gaps were varied and patchy. In some places there was an initial flush of ground plants, which gave way to coarser, more competitive ground plants, and in turn these gave way to regeneration of trees. But there were many variations on this: sometimes with fallen trunks blocking all vegetation; sometimes with coarser ground plants not being replaced; sometimes with understorey bushes present prior to gap creation coming to largely fill gaps; or sometimes large herbivores prevented woody species developing and facilitated the development of grassland. Tree regeneration was distinctly patchy with a range of factors inhibiting the abundance of seed and the establishment and growth of seedlings.

Canopy gaps are commonly the focus of tree and shrub regeneration/development in natural temperate woodland reflecting a general increase in light, moisture and other resources. However, given the variability of the numerous interactive factors and processes that control vegetation growth and regeneration in gaps, combined with the patchiness of inherited features and site conditions within and around gaps, it notoriously difficult to predict precisely what vegetation and regeneration will develop within any one gap, though there are distinct trends (see Watt 1923-25, Canham & Marks 1985, Connell 1989, Platt & Strong 1989, Veblen 1992, Harmer & Kerr 1995, Oliver & Larson 1996, Peterken 1996, Smith *et al.* 1997). It should be possible to develop a computer model to take account of the major variables involved and make better predictions of regeneration in canopy gaps, though quantitative information on many of the controlling parameters is limited (Price *et al.* 2001).

4.3.8.3. Release of overstorey trees around larger canopy gaps

Overstorey trees also responded to the creation of canopy gaps by growing into the vacated space. In small gaps they did this mainly by extending their crown branches. In somewhat large gaps they also tended to develop epicormic sprouts on the crown branches, and in even larger gaps (notably the windstorm gaps created at The Mens) they produced sprouts on the middle and/or upper trunk or even extended from low lateral branches. This appeared to be controlled largely by the amount of additional light reaching the branches or trunk. However, many trees had already developed epicormic sprouts and latent buds in response to exclusion, which appeared to give them a distinct advantage when released. Moreover, beech had a tendency to fill parts of gaps by from low lateral branches it had retained below closed stands, whilst epicormic trunk/crown sprout growth was especially important for oak.

Such a response can be readily observed in deciduous British woodland. In the present study it was recorded on canopy trees in part-broken stands and especially around windstorm gaps at The Mens. It was recorded on oak, beech and other species at Denny, Langley Wood and Clairinsh, as it has elsewhere (Mountford *et al.* 2001b, Mountford & Ball 2004, Mountford unpublished data). It is recognised as an important mechanism for trees to forage for light (e.g. Young & Hubbell 1991, Young & Perkocha 1994). In experimental gaps in mixed hemlock-hardwood stands in eastern North America, Muth & Bazzaz (2002) detected different responses of gap-edge trees related to their species and canopy position: in general sub-canopy trees and pioneer species showed greater displacement and precision of growth into gap centres than canopy trees and shade-tolerant, late-successional species. These aspects deserve further study in British and nearby continental woods.

4.4. Structural development of natural stands

This section deals with the third major part of the thesis, the structural development of natural stands. This was recorded at all of the study sites in terms of the basal area, density, size and stratification of stems, the extent of canopy gaps, and the volume of dead wood. In the following sections these aspects are summarised, compared to relevant literature, and a synthesis is presented of the general structural development of natural stands in native deciduous woodland in Britain.

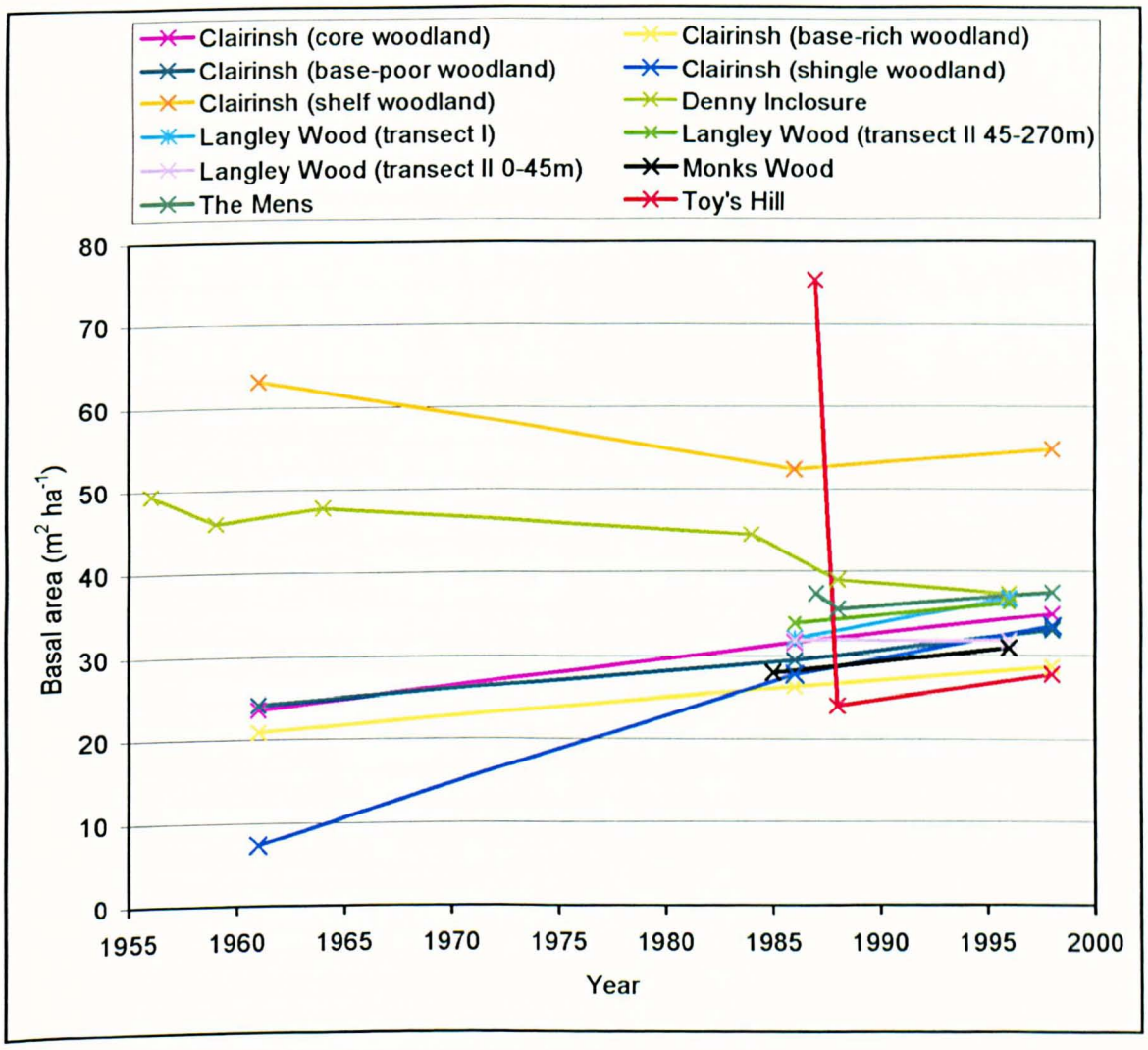
4.4.1. Changes in stand basal area

In many of the stands studied, the combined basal area of stems tended to increase over time (Figure 4.1), reflecting the fact that more biomass was accumulated through growth that was lost through exclusion. At Denny, however, the basal area tended to decline as it was set back by mortality caused by drought, wind damage and debarking. The basal area also declined slightly at The Mens as a result of mortality caused by the 1987 windstorm, but this was recovered within a decade. The basal area in the shoreline shelf woodland at Clairinsh also tended to decline slightly, though the basal area values were rather high because the area sampled was small and included a large oak tree. The exception was Toy's Hill where the basal area declined dramatically due to severe wind damage in 1987.

There was a general convergence in the basal area levels recorded, with most stands at 28-37m^2 ha^{-1} in 1996-8 (see Figure 4.1). Accepting that the area sampled for each stand was not the same and that individual transect sections within specific stands included a range of basal area values (especially at Denny), this still gives an indication of the basal area range that can be expected in mature or partially collapsed old-growth stands in lowland Britain.

The maximum basal area recorded in the stands under study was compared to those reported in other minimum-intervention reserves in lowland Britain and continental

Figure 4.1: Summary of the trend in the stand basal area over time in the minimum-intervention reserves recorded for this study



north-west Europe (see Table 4.3). These sites represented a range of stand types at various stages of development and degrees of disturbance. Those at the lower end of the range included stands that were either still maturing and had been only part set back by disturbances (e.g. Monks Wood, Lady Park Wood young-growth stands), that had matured and then collapsed on a large scale (e.g. Fontainebleau, stands below cliff at Lady Park Wood), or had only part-filled with trees (e.g. base-rich woodland at Clairinsh). At the other end of the range, the three sites where the basal area exceeded $60m^2\ ha^{-1}$ were atypical because they were sampled by small or narrow plots and/or dominated by peculiarly large trees (Toy's Hill). At the remaining sites the maximum basal area recorded was between $30\text{-}50m^2\ ha^{-1}$. This range can be taken as indicative of the maximum basal

area typically attained by old stands under natural conditions in lowland Britain before they start to break-up.

Table 4.3: Summary of the maximum stand basal area as recorded in minimum-intervention reserves in lowland Britain and continental north-west Europe. The sites represent a range of maturing and old stands, some of which have been damaged by disturbances. The minimum stem size used was ≤5cm dbh, except for Draved Skov where it was 10cm dbh

Site	Maximum recorded basal area (m^2 ha^{-1})	Source
Lady Park Wood (slopes below cliff, old-growth)	21	Mountford (unpublished data)
Lady Park Wood (young-growth)	23	Mountford (unpublished data)
Fontainebleau (plot 2, La Tillaie)	27	Wijdeven (2003a)
Draved Skov (Carlsberg enclosure)	27	Wolf (2002)
Clairinsh (base-rich woodland)	29	This study
Hasbrucher Urwald (transect II)	29	Wijdeven (2003c)
Fontainebleau (plot 1, La Tillaie)	29	Wijdeven (2003a)
Zoniënwoud	30	Van den Berge *et al.* (1990)
Lady Park Wood (upper steep slopes, old-growth)	30	Mountford (unpublished data)
Monks Wood	31	This study
Buckholt Wood	31	Mountford (2003a)
Langley (transect II, 0-45m)	32	This study
Draved Skov (Lime enclosure)	32	Wolf (2002)
Pijpebrandje	32	Wijdeven (2003b)
Clairinsh (base-poor woodland)	33	This study
Clairinsh (shoreline shingle woodland)	33	This study
Neuenburger Urwald	34	Wijdeven (2003c)
Lady Park Wood (mid-slopes, old-growth)	34	Mountford (unpublished data)
Lady Park Wood (plateau above cliff, old-growth)	34	Mountford (unpublished data)
Noar Hill (main slopes & upper plateau)	35	Mountford (2004)
Het Rot	35	Clerkx *et al.* (2001)
Clairinsh (core woodland)	35	This study
Lady Park Wood (upper plateau, old-growth)	36	Mountford (unpublished data)
Langley (transect II, 45-270m)	36	This study
Langley TI	37	This study
The Mens	37	This study
Suserup Skov (part C)	38	Emborg *et al.* (1996)
Suserup Skov (part A)	39	Emborg *et al.* (1996)
Ridge Hanger (Ashford Hangers)	39	Mountford & Ball (2004)
Dendles Wood	42	Mountford *et al.* (2001)
Lady Park Wood (plateau above cliff, old-growth)	44	Mountford (unpublished data)
Suserup Skov (part B)	48	Emborg *et al.* (1996)
Denny Wood (unenclosed transect)	48	Mountford & Peterken (2003)
Denny Inclosure	49	This study
Clairinsh (shoreline shelf woodland)	63	This study
Hasbrucher Urwald (transect I)	66	Wijdeven (2003c)
Toy's Hill	75	This study

These two ranges of c.30-40/50m^2 ha^{-1} are similar to typical maximum values reported from other old-growth mixed deciduous stands, including mixed mesophytic stands in

eastern North America (21-42 m^2 ha^{-1}) (Parker 1989, Martin 1992), beech-oak and beech stands in east-central Europe (30-49 m^2 ha^{-1}) (Korpeľ 1982), and lime-hornbeam stands in Białowieża Forest (34-39 m^2 ha^{-1}) (Faliński 1986, Bernadzki *et al.* 1998, Nilsson 2003).

4.4.2. Changes in stem density, size and stratification

As even-aged groups matured within the stands studied, there was a general increase in top height, a decrease in stem density, and a shift in the stem size-distribution from negative exponential to normal right-skewed, i.e. very small stems decreased greatly, small stems remained relatively numerous, and some medium and a few large stems developed. In addition, there was a great of deal of variation in height growth both within and between species, which presented an opportunity for a series of stratified layers to develop.

The size-distributions that developed in each species population depended on their intrinsic rate of growth and tolerance to overtopping. However, in many cases this and the decline in stem density and degree to which stands stratified was greatly affected by the dominance of shade-tolerant overstorey trees. For example, where beech was prominent at Denny and The Mens then exclusion was more pronounced and light-demanding trees and shrubs were eradicated much more readily. Where light crowned trees dominated or were at least prominent in mixed stands then survival in the substratum was much greater. Thus, stem density remained high and the stands tended to develop a much greater degree of stratification. This was exemplified at Monks Wood, though even here the distribution of understorey individuals was patchy.

The decline in stem density was reversed in mature stands where the understorey expanded/invaded. This increased stratification and also affected the size-distribution of stems as once again very small stems became prolific and a negative exponential distribution developed, even though the population as a whole comprised at least two

distinct age groups. At Denny (and to a lesser degree at Monks Wood) this process was set back greatly by ponies and/or deer and the understorey was largely wiped out. Where stands broke-up due to windstorms or severe drought there was an immediate fall in density, larger trees and stratification. Large wind damaged trees often took out some medium and small stems as they fell, reducing density across the size-range.

The largest individual trees recorded across the sites included beech up to 570cm gbh (180cm dbh), oak to 400cm gbh (130cm dbh), ash to 215cm gbh (70cm dbh), birch, field maple and holly to 160-170cm gbh (50-55cm dbh), hawthorn to 95cm gbh (30cm dbh), and hazel to 65cm gbh (20cm dbh). Beech, birch and hazel are unlikely to get much larger, but the other species could. Oak might develop trees with exceptionally large trunks, especially if can develop in a pollard-like form. Whatever, large trees will remain scarce.

Thus, even-aged stands tend to pass through a prolonged phase where exclusion remains dominant, the density of stems declines and the size-distribution becomes right-skewed and truncated in the very smallest classes. In mixed light-canopied stands a series of stratified layers can be expected to develop. During the latter stages of stand maturation, stem density and stratification tend to increase and the size-distribution returns to a negative exponential. Only a few large trees ever develop. These general trends are widely recognised aspects of stand maturation in natural temperate woodland (Oliver & Larson 1996, Peterken 1996).

4.4.3. Changes in canopy gaps

Canopy gap formation was a major process governing growth, mortality and regeneration. Gaps arose where overstorey trees were killed or damaged by windstorms and drought and, less often, by grey squirrel debarking or other factors. They were filled by the release of suppressed trees, regrowth of damaged trees or the expansion of border-trees. The extent of

gaps recorded at the study sites is summarised and compared with other minimum-intervention reserves in lowland Britain and continental north-west Europe in Table 4.4. This indicates that gaps have usually remained limited for many decades whilst stands have being maturing, but they have increased thereafter and sometimes become extensive.

Table 4.4: Summary of the extent of canopy gaps as recorded in minimum-intervention reserves in lowland Britain and continental north-west Europe. The sites represent a range of maturing and old stands, some of which have been damaged by disturbances

Site	Extent of canopy gaps in area studied	Age of dominant trees in stand	Main cause of gap formation	Reference
Lady Park Wood (old-growth stands on plateau above cliff)	0% (in 1983) 0% (in 1992) 0% (in 2000)	Few trees 150-250 but most 80-125 years old	None (stable beech stand on deep soils)	Mountford (unpublished data)
Monks Wood	10%	Few trees 100-200 but most 80 years old	Wind damage/stem collapse (ash), ride management, also drought (birch)	This study
Fontainebleau (plot 2)	10% (in 1983) 2% (in 1991) 5% (in 2000)	Mix of trees from 50/150-300/400 years old	Wind damage (beech, oak)	Wijdeven (2003a)
Pjperbrandje	10% (in 1983) 2% (in 1991)	Some trees 200/250 but many 100/140 years old	Wind damage (beech)	Wijdeven (2003b)
Langley Wood	12%	Few trees 150-300 but most 60 years old	Wind damage (birch, oak)	This study
Suserup Skov	8% (in 1992) 14% (in 2000)	Mix of trees from 35-280 but mainly 120-220 years old	Wind damage (beech, ash, elm)	Emborg *et al.*(2000, 2002)
The Mens	17%	Some trees >200 but many 150 years old	Wind damage (beech, oak), also grey squirrel debarking (beech)	This study
Lady Park Wood (young-growth stands)	18% (in 1985) 10% (in 1993)	Few trees 75-300 but most 40-50 years old	Drought (birch, beech), also Dutch elm disease, grey squirrel debarking (beech), wind damage (birch, beech)	Peterken & Jones (1989), Mountford (1994)
Clairinsh (core and base-poor woodland)	16-21%	Mix of trees from 85-200/300 years old	Wind damage (oak), also felling of exotic trees, crown deterioration (oak)	This study
Dendles Wood	20%	Some trees >200 but most 150 years old	Wind damage (beech), also grey squirrel debarking (beech)	Mountford *et al.* (2001)
Fontainebleau (plot 1)	6% (in 1983) 7% (in 1991) 23% (in 2000)	Mix of trees from 50/150-300/400 years old	Wind damage (beech)	Wijdeven (2003a)
Lady Park Wood (old-growth stands on mid- & upper slopes/plateau)	27% (in 1983) 15% (in 1992) 8% (in 2000)	Few trees 150-250 but most 80-125 years old	Drought (beech), also wind damage (ash)	Mountford (unpublished data)
Denny Inclosure	30%	Some trees >250 but many 125 years old	Drought (beech), also wind damage (beech, oak), grey squirrel debarking (beech)	This study
Lady Park Wood (old-growth stands below cliff)	43% (in 1985) 31% (in 1992)	Some trees 100-200 but many <40 years old	Dutch elm disease, also collapse/wind damage (ash, beech)	Mountford (unpublished data)
Denny Wood	64%	Half-collapsed stand with some trees >250, others 80-150 years old	Drought (beech), also salvage felling, wind damage (oak), grey squirrel debarking (beech)	Mountford & Peterken (2003)
Toy's Hill	98%	Collapsed 60-150/200 year old stand	Wind damage (beech, oak)	This study

Certainly, gaps remained scarce in the maturing stands at Monks Wood (see Figure 3.4.3): the most extensive gaps present in 1996 appeared to be associated with ride management at the end of one of the study transects where couple of large oak had been removed before 1985. Gaps also remained scarce and small at Langley Wood (see Figure 3.5.4). Much of the canopy remained closed at Clairinsh through to 1998 (see Figure 3.6.7), albeit that a wide scatter of relatively small gaps was created by wind damage and (in later years) where canopy trees deteriorated or non-native species were felled. In 1998, gaps covered 16% of transects in the core woodland and 21% in the base-poor marginal woodland, and many older gaps had been substantially closed. In contrast, the canopy failed to completely close and remained noticeably broken towards the shoreline and base-rich woodland at the north end of the island.

At The Mens, a scatter of gaps were made by thinning operations in the 1950/60s, but these closed over within a couple of decades. More were, however, opened by the 1987 and later windstorms and by 1998 gaps covered 17% of the circular study plots. The main gaps formed in 1987 and their closure to 1998 was recorded in some detail. They initially ranged from 115-1090m^2 and all had part-closed by 1998. This was mainly due to the lateral extension of bordering beech and oak, typically at a rate of 10-40cm per year. Similar rates have been recorded for a few oak and beech in Lady Park Wood (Mountford unpublished data). The only other records of border-tree expansion rates that could be traced were for various deciduous tree species in eastern North America: these had quite similar maximum rates of 17-59cm and 20-26cm and average rates of 8-14cm, 9-31cm and 10-18cm (Hibbs 1982, Runkle & Yetter 1987, Runkle 1998).

The expansion of border-trees at The Mens resulted in gaps closing by 4-33m^2 per year, with the larger gaps generally closing more. The main exceptions were two gaps that were strongly filled below by beech. The net area each gap closed was, however, curtailed

because several border-trees were uprooted, snapped or lost branches. This was mainly due to further wind damage, but grey squirrel debarking lead to the death of a few beech and caused branch snapping in other border beech. Typically the newly opened areas were limited to no more than $60m^2$, but in one case $126m^2$ was opened. In addition, two smaller gaps were joined because of the loss trees between them. This confounds any predication of the time it might take for the gaps to close. In addition, gap shapes and the expansion of border-trees was irregular (Figure 3.2.5a), linear gaps and narrow corners will probably fill more rapidly than circular and convex edges (Figure 3.2.5b), the largest two gaps were certainly too wide to be filled completely by border-trees (Figure 3.2.5d), and the rate of crown expansion will probably decrease with time (Runkle 1998). Thus, although some of the smallest gaps might close within two decades of creation, others will probably take at least a few decades, and some will only be closed by regeneration within the gap.

In a study of gap closure in mixed beech-ash-oak-chestnut stands in southern England, Valverde & Silvertown (1997) estimated that gaps of about $400\text{-}450m^2$ would take only between nine-eighteen years to close. However, this study was based on a chronosequence time-series of hemispherical photographs, closure was based on the degree of canopy openness not the extent of gap margins, and they used a constant percentage decline rate and no allowance was made for any further opening. Circular gaps of this size in southern Appalachian woods (North America) ought to take 95-100 years to close over by border-trees based their 12cm per year average lateral extension rate (Runkle 1998) and assuming a constant annual reduction in the gap radius (Runkle & Yetter 1987). Gaps in these woods are also often enlarged by the death of border-trees due to wind damage: in a fourteen-year study of 250 canopy gaps undertaken by Runkle (1998), 46% of the gaps were affected by border-tree mortality. Although this means gap closure could take even longer, openings in these woods are often $<400m^2$, they fill quickly with well-developed advance regeneration, and gaps of more than about ten years are rare (Barden 1980, 1981, 1989, Runkle 1981,

1982, 1990, Runkle & Yetter 1987). Interestingly, Runkle (1998) found that the mortality rate for border-trees was no higher than for canopy trees in general, but was a reflection of the frequency with which trees bordered gaps. Even so, at The Mens it appeared that increased exposure at gap edges was important in explaining much of the border-tree damage.

Gap creation was somewhat more extensive at Denny (see Figure 3.1.6) than Clairinsh, Langley Wood, Monks Wood and The Mens. By 1996 gaps covered 30% of the study transect, mainly due to the death of pre-1750 beech killed by drought (most stands that regenerated around 1870 remained intact). Almost the same extent of gaps was recorded in the old-growth stands on the mid- & upper slopes/plateau at Lady Park Wood, which was also mainly due to the death of old beech following the 1976 drought. However, these were more scattered than at Denny. As significant was the 18% gaps recorded in the young-growth stands here, which were only about thirty years old when they suffered massive die back of birch in 1976. Since this time gaps in both of the stands have substantially filled.

Three of the sites in Table 4.2 have had more extensive gaps recorded, including the old beech stands at Toy's Hill and the unenclosed part of Denny Wood. The stands at Toy's Hill had closed after having had some trees cut in it in the early 20th century, but were largely blown over in October 1987. Extensive gaps were also created by the 1987 windstorm in old beech stands at Noar Hill and Ashford Hanger reserves (Mountford 2004, Mountford & Ball 2004). In the unenclosed part of Denny many old beech died due to the 1976 drought and gaps opened widely. However, a safety felling operation was undertaken and this might have involved taking down some sub-lethally damaged trees, opening gaps more widely that would have happened naturally. The third site Lady Park Wood where as much as 43% gaps was recorded in the stands below the cliff line. These occupy steep

slopes and were extensively opened following the decline of many of the elm present to Dutch elm disease, combined with the occasional fall/windthrow of large trees.

The percentage of canopy gaps recorded at most of the sites listed in Table 4.2 is similar to that reported from old-growth stands in eastern North America, where sporadic wind damage is also the main agent of canopy disturbance: in a study of fourteen stands Runkle (1982) found gap openings covered 3-24% (average 9.5%) of the area, whilst Tyrrell & Crow (1994) found they covered 3-17% in twenty-five other stands and the percentage increased linearly with stand age. Nevertheless, occasional catastrophic blow downs associated with hurricanes are also reported from these woods, in some cases stretching several hundred hectares (Lorimer & White 2003).

Thus, it seems that gap creation in natural stands in Britain is predominately, though not always, associated with mature stands beyond about 125-150 years growth. Even in old stands gap creation tends to be patchy and with periods of gap closure taking takes place between episodes of gap creation. Nevertheless, extensive gaps can be formed in old stands, particularly where beech is abundant and forms extensive stands. Small gaps can close within two decades of creation by the expansion of border-trees, but medium-sized gaps will take at least a few decades to close. Larger gaps will only be closed by tree regeneration within them, and in some gaps closure is likely to be delayed by subsequent damage to border-trees. Gap creation is dependent mainly upon the impact of windstorms and drought, but grey squirrel debarking and other agents can open gaps, notably Dutch elm disease.

4.4.4. Changes in dead wood

The volume of dead wood recorded at each of the study sites is summarised and compared with levels reported at other sites in lowland Britain and continental north-west Europe in

Table 4.5. It remained low at Langley Wood and Clairinsh and not much higher at Monks Wood, with similar levels having been recorded in various maturing stands that have suffered little or only a limited of disturbance. The input of dead wood at these three study sites largely a product of exclusion in maturing stands, which generated predominately small snags and logs that decayed quickly. The most significant input of dead wood occurred at Monks Wood and was associated with the 1976 drought. However, even this was only moderate and appeared to have decayed very quickly as it was mainly birch. Nevertheless, there were signs that the volume here had started to increase as the stands had matured and some larger trees were starting to die off.

The volume of dead wood was considerably higher at The Mens. Before the 1987 dead wood had been relatively limited here too, but wind damage in this and later years brought down a good many large trees and branches increasing the volume to over $100m^3\ ha^{-1}$. Similar volumes of dead wood have been created in other reserves where wind and/or drought have killed a scatter of large trees (Table 4.5). At Denny Inclosure drought damage was more severe and some additional trees were toppled in windstorms. Thus, the dead wood volume was even greater here and comparable will other beech reserves at Fontainebleau, Ashford Hangers and Noar Hill Hangers where severe windstorm damage has generated a glut of dead wood (see Table 4.5). The volumes for all these sites are not dissimilar to the range reported for various old-growth reserves in east-central Europe (58-$296m^3\ ha^{-1}$ snags and/or logs) and eastern North America (46-$137m^3\ ha^{-1}$ logs, c.50-$200m^3\ ha^{-1}$ snags and logs) (see Tyrrell & Crow 1994, Peterken 1996, Kirby *et al.* 1998, Christensen *et al.* 2004). The value for Toy's Hill was, however, extreme with the 1987 windstorm having converted most of the former stand here to dead wood.

There were clear signs that the volume of dead wood at The Mens, Denny and Toy's Hill would decline in the near future. Many of the beech logs generated immediately after the

Table 4.5: Summary of the volume of dead wood as recorded in minimum-intervention reserves in lowland Britain and continental north-west Europe. The sites represent a range of maturing and old stands, some of which have been damaged by disturbances

Site	Snags & logs (m^3 ha^{-1})	Logs (m^3 ha^{-1})	Comments	Source
Various sites around Britain	-	10-59	Maturing, derelict coppice or unmanaged high forest	Green & Peterken (1997), Kirby *et al.* (1998)
Lady Park Wood (young-growth)	15-32	11-26	Part-damaged by drought and other agents	Green & Peterken (1997)
Clairinsh	19	12	Part-damaged by wind	This study
Langley Wood	22	15	Part-damaged by wind	This study
Lady Park Wood (old-growth)	35	15	Undamaged	Green & Peterken (1997)
Monks Wood	37	25	Part-damaged by wind	This study
Pijpebrandje, Netherlands	43	32	Part-damaged by wind	Christensen *et al.* (2004)
Weversbergen, Netherlands	48	46	No information on distrubance	Christensen *et al.* (2004)
Dassenberg, Netherlands	61	43	No information on distrubance	Christensen *et al.* (2004)
Gortel, Netherlands	65	56	No information on distrubance	Christensen *et al.* (2004)
Møns Klinteskov, Denmark	73	48	No information on distrubance	Christensen *et al.* (2004)
Knagerne, Denmark	87	56	No information on distrubance	Christensen *et al.* (2004)
Lady Park Wood (old-growth)	87-112	46-81	Part-damaged by drought & windstorms	Green & Peterken (1997)
Velling, Denmark	99	68	No information on distrubance	Christensen *et al.* (2004)
The Mens	115	88	Part-damaged by wind	This study
Dendles Wood	128	62	Part-damaged by wind	Mountford *et al.* (2001)
Great Monk Wood	-	95	Part-damaged by wind	Kirby *et al.* (1998)
Strødam Reservatet, Denmark	139	101	Part-damaged by wind	Christensen *et al.* (2004)
Zoniënwoud, Belgium	142	111	Part-damaged by wind	Van den Berge *et al.* (1993), De Keersmaeker *et al.* (2002
Cotswold beechwood	-	139	Damaged by wind	Kirby *et al.* (1998)
Suserup Skov, Denmark	163	154	Damaged by wind	Christensen *et al.* (2004)
Fontainebleau, France	100-178	92-256	Damaged by wind	Koop & Hilgen (1987), Mountford (2002a), Wijdeven (2003a)
Denny Inclosure	278	187	Severely damaged by drought & wind	This study
Ashford Hangers	203-322	200-319	Severely damaged by wind	Mountford & Ball (2004)
Noar Hill Hangers	351	309	Severely damaged by wind	Mountford (2004)
Toy's Hill	500	470	Severely damaged by wind	This study

1976 drought at Denny had already substantially decayed by 1996, and many of those killed later here and elsewhere in the 1980s had decay setting in within a decade of creation. This is supported by observations in Dutch woodland reserves where large beech trunks have largely decayed away within three or four decades of formation and species

decay rates have ranked beech >birch >oak (Van Hees & Clerkx 1999). This suggests that at Toy's Hill the huge volume of dead wood here will mostly disappear within a few decades and remain low for many decades thereafter. This will be less critical at Denny and The Mens as there are still large trees left here to top up the dead wood that decays and a greater portion of the dead wood is in oak, which was the only major species found to be generally resistant to decay. Oak has also been found to be more resistant to decay in Dutch woodland reserves (Van Hees & Clerkx 1999) and also in eastern North America, due particularly to the fragmentation of beech logs (MacMillan 1988).

Thus, the volume of dead wood in natural stands tends to be inversely related to the basal area of live trees. It is high immediately after a major disturbance and declines to a low level during the stem exclusion stage as the original fallen trees decay and only small material is input by exclusion. The dead wood volume increases again as stands become mature and large overstorey trees start to die (see Bormann & Likens 1979, Koop & Hilgen 1987, Mountford 2002b). The volume created by disturbances depends on their scale and frequency. Where disturbance is small-scale and infrequent the volume of dead wood in old stands will be moderate but sustained. Large-scale disturbances will generate a temporarily high volume of dead wood.

4.4.5. Developmental stages

The key processes and features of stand development recognised in the preceding sections were organised into four developmental stages. These are shown schematically in Figure 4.2 and described in Table 4.6. They broadly encompass the natural development of mixed native deciduous stands on mesic sites in lowland Britain, from their initiation to break-up and round again. The stages follow the scheme outlined in Figure 1.1, but are based primarily on those identified for temperate woodland in eastern North America by Oliver (1981)/Oliver & Larson (1996) and adapted by Peterken (1996). This was preferred

because, compared to the schemes used for east-central Europe (e.g. Leibundgut 1982, Mayer 1984, Průša 1985, Korpeľ 1995), the approach and terminology focused primarily on processes rather than structural development and fitted most readily with the observations made in this study.

The key processes and features identified for each stage change over time, starting with regeneration and release in gaps, then stem exclusion in closed stands, understorey regeneration and release in mature stands, and finally natural disturbance and senescence in old stands. The stages are, of course, a broad generalisation. The composition and precise definition of each stage will vary from place to place, and certain factors and stages will be more important in certain stand types and situations. In some situations certain phases may be bypassed (e.g. by severe wind damage to young stands) or prolonged (e.g. where grazing/browsing prevents understorey reinitiation and gap-phase regeneration). Nevertheless, they serve as an initial general framework to place stand dynamics in native British woodland.

Several notable processes and features arise from those amongst identified in Table 4.6. Firstly, stand initiation can be highly modified by large herbivores and an open phase can occur, in which tree and shrub regeneration is prevented and areas of grassland and bracken can spread extensively as happened at Denny study site. This is most likely on sites that are formally treated as wood pastures, with livestock being deliberately set out in addition to free-ranging deer. However, given the recent general increase in deer around the country, this may also become an increasingly important issue at other reserves, as is the case with Lady Park Wood where fallow deer have become numerous (Peterken & Mountford 2002). Where large herbivores are maintained at a high level then stand initiation may be prohibited and protracted open phase might ensue. If herbivores are somewhat less abundant, then regeneration might develop in places, especially of less

Figure 4.2: The four main developmental stages recognised in this study for minimum-intervention reserves in lowland Britain and continental north-west Europe. The key processes and features of each stage are described in Table 4.6. Although the diagram is broadly applicable and depicts one possible realistic scenario based on changes in a mesotrophic mixed stand of beech (orange trees), birch (light blue), ash (hatch), oak (green) and holly (black), the composition of each stage will vary from place to place and certain factors and stages will be more important in certain stand types and situations (see text for details).

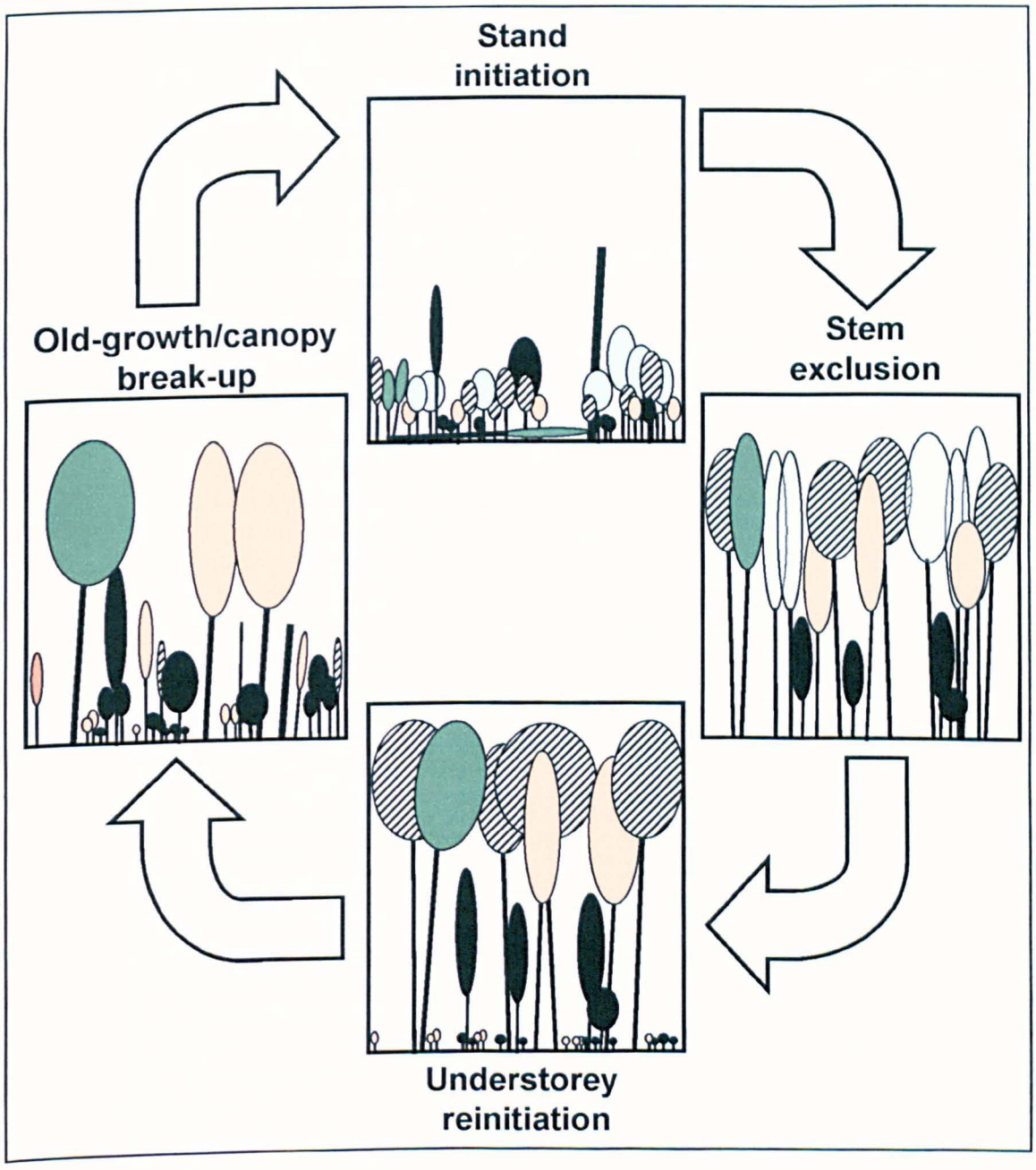


Table 4.6: Summary of the key processes and features in each of main developmental stages recognised in minimum-intervention reserves in lowland Britain and continental north-west Europe

Stage	Key features
Stand initiation stage	• This occurs after canopy break-up and is concerned with the development of vegetation and regeneration within canopy gaps • In large well-lit gaps there is a potential for well-dispersed, light-demanding trees and shrubs to regenerate abundantly • Smaller gaps tend to be filled by expanding border-trees and below by species that are more tolerant of shade, especially from advance regeneration and bushes present below the previous stand • Several legacies will be retained from the previous stand – this will normally include some or many live trees and shrubs, some of which will have been uprooted, snapped or crushed during gap creation, some of which will recover and expand or will be 'released' into vigorous growth – released poles of beech and other species are vulnerable to squirrel debarking – in addition some or much dead wood will be retained • Tree regeneration can be abundant in gaps, but often they fill partly or more substantially with shrubs, ground vegetation, fallen live trees, piles of fallen dead wood/brash, and root plates/pits • Gap-phase regeneration (and release) is likely to involve a good deal of vegetative growth and develop not just from seedlings • Regeneration is controlled by a wide range of factors, not least light availability, seed/sprout/sucker production, seed dispersal and predation, conditions that permit establishment and growth, browsing and debarking, and the development of the gap opening over time – it can be highly modified or prevented by large herbivores and instead a protracted open phase can occur
Stem exclusion stage	• This occurs after the stand initiation stage and is concerned with developments in maturing closed stands • Exclusion is normally the dominant process – it tends to result in the death or at least the suppression of less vigorous, slower-growing and/or more light-demanding stems – the most vigorous trees are left to grow into large dominant individuals – it is a gradual process so the canopy stays closed and regeneration is prevented • The extent to which light-demanding species are excluded depends on the dominance of shade-tolerant trees, notably beech and lime – where these are abundant (not all native stands are dominated by such trees), light-demanding shrubs suffer from exclusion and light-demanding trees have to grow tall to survive • Stands get taller and tend to develop a series of stratified layers – this is dependent on the shade cast by overstorey trees, the shade-tolerance of species in the substratum, and variation in the height growth of individuals/species – stratification tends to develop best under light crowned trees (ash, birch) and where reasonably shade-tolerant shrubs and medium-tall trees are prominent • Stem basal area tends to increase whilst stem density goes down – the stem size-distribution changes from negative exponential to right-skewed • Disturbance tends to be limited, but sometimes stands are substantially affected by drought, wind damage, Dutch elm disease, or debarking by grey squirrels/large herbivores – this depends on the tree/shrub species present, their vulnerability and the severity of such disturbances • Dead wood normally declines as logs from the previous stand rot away and only small material is input from exclusion

Continued overpage

Table 4.6: continued

Understorey reinitiation stage	• This occurs in mature stands where the overstorey opens slightly and loses its grip on the understorey – this allows relatively shade-tolerant understorey shrubs and trees (and ground plants) to expand and/or invade (reinitiate) in the understorey • It happens as pioneer trees die out, longer-lived trees start to decline in vigour and show the effects of climatic stress (drought, wind damage), and minor canopy disturbances have a more sustained impact – it can release pole trees and encourage grey squirrel debarking – although exclusion becomes less significant it nevertheless continues to be important • It generally starts after about 50-100 years of development during which stem exclusion is dominant, but the transition can be gradual, subtle and patchy – it depends greatly on the species dominating the overstorey, the shade they cast, how disturbances impact, how abundant pioneer trees, longer-lived shade-tolerant trees and shade-tolerant shrubs are, and to what extent suppressed sub-canopy trees replace pioneer trees – it can last for many decades or be cut short by more significant disturbances • Understorey shrubs and trees (and ground plants) may develop as short advance regeneration or grow into saplings, poles and sizeable bushes – as they develop stand stratification becomes increasingly complex – the development of the understorey depends on a wide-range of factors as in stand initiation – it can be highly modified, prevented or set back by large herbivores • Stand height and basal area tend to peak and dead wood volume starts to increase
Old-growth/ canopy break-up stage	• This represents the stage when dominant overstorey trees deteriorate or are lost to senescence or disturbances, principally severe windstorms or drought, and larger gaps are created – it eventually takes stands to the stand initiation stage and tends to begin when stands reach at least 125-150 years growth • Canopy break-up can be slow, rapid, progressive, irregular, and create gaps of many sizes – it can produce a fine-scale, coarse-grained or irregular mosaic – the actual pattern that develops depends on a host of factors including what species predominate, how long each will live, their vulnerability to disturbances, the vulnerability of the site they occupy, and the frequency and severity of disturbances • Stands become more vulnerable to break-up the older and larger the trees therein get – mature beech are particularly vulnerable to drought and wind damage – mature oak are less vulnerable to drought, seem more stable and better-adapted to shed crown branches during windstorms and resprout afterwards • Severe climatic events can cause extensive break-up in lowland Britain, but it seems that most often break-up is irregular and protracted creating mainly small-medium gaps and sometimes with a few large gaps • Canopy break-up caused by windstorms will leave some overstorey trees uprooted and others broken, and create root mounds and pits – individuals in the substratum are prone to damage from falling branches and trunks • The basal area of live stems falls, but the volume of dead wood is increased as is the abundance of large snags and logs

palatable woody species and in the protection of prickly bushes and other features as postulated by Morgan (1987b) and Vera (2000). Even at relatively low levels, large herbivores might limit regeneration of highly palatable species.

Secondly, canopy gaps can be filled not only by tree regeneration, but also by: (i) crown expansion on border trees, which will be especially important in small, narrow gaps; (ii) shrubs, especially of more shade-tolerant species (notably holly, hazel, hawthorn) that are present in the understorey before gap creation; (iii) fallen live trees, which in some cases may sprout strongly and lead any regeneration; and (iv) ground vegetation and piles of fallen dead wood/brash, which might limit regeneration of trees and shrubs and maintain open conditions. In addition, a good deal of the regeneration in gaps is likely to be vegetative, including the recovery of individuals crushed and broken during gap creation. In natural stands in Britain, it would be misplaced to simply think of canopy gaps being filled with tree seedling regeneration, as is the usual aim in managed stands restocked by natural regeneration.

Thirdly, stand development can be highly modified by debarking by American grey squirrels. This can have a profound affect on vigorous pole-sized stems of beech and other species, with only ash and lime amongst the main broadleaves appearing much less susceptible (Mountford & Peterken 1999). This is a recent but widespread phenomenon that seems set to profoundly change the course of natural stand development within many native stands. It remains unclear just how many developing trees will be adversely affected and if severely debarked individuals will survive or recover from this.

Fourthly, the number of native woody species is relatively low in Britain, especially compared to eastern North America. Moreover, tall shade-tolerant trees do not dominate some native woodland types, partly because lime and wych elm have been reduced, but also because beech, hornbeam and sycamore have not spread into all sites they might occupy (Rodwell 1991, Peterken 1993a, Rackham 2003). Such stands tend to retain a substratum of moderately shade-tolerant shrubs and medium trees during the stem exclusion stage. Normally, these would be excluded in stands dominated by shade-tolerant

trees, as exemplified by natural stands of beech-fir-spruce in central Europe (e.g. Průša 1985, Korpeľ 1995). As stands progress into the understorey reinitiation and old-growth/canopy break-up stages, such individuals will be released and could potentially fill gaps. This could result in areas being dominated by shrubs rather than tall trees. This is significant, as it demonstrates a feature not widely appreciated and one that helps explain the surprising abundance of hazel in original-natural woodland (see Rackham 2003).

A fifth notable aspect is the vulnerability of mature beech stands to break-up during severe drought and windstorms. This shade-tolerant tree commonly dominates mature stands in Britain where it is present. It is also a major species in other parts of Europe, particularly submontane and montane areas of central and east Europe (Jahn 1991). In Britain, unlike central and east Europe, beech stands are prone to sudden and quite extensive collapse, as evidenced by the impact of the 1987 windstorm at Toy's Hill and the 1976 drought at Denny study sites. This can advantage other species, especially oak, which often struggles to compete with beech in closed stands, but which can outlive it by several centuries.

The minimum-intervention stands included in the present study had inherited various large blocks dominated by or with a substantial component of even-aged growth. Although their development showed a degree of uniformity, there was nevertheless some irregularity and certainly once stands started to break-up. This was related to inherent variations within the initial stand structure and composition, the underlying soil conditions, seed immigration and establishment, the incidence of wind and drought damage, and other factors. It would be useful to map and examine this spatial mosaic pattern across reserves, based on the developmental stages outlined in Table 4.6. This has been done in many reserves in east-central Europe (e.g. Leibundgut 1982, Mayer 1984, Průša 1985, Korpeľ 1995). It would extend the patterns mapped along the narrow transects used in this study and provide useful information on the spatial pattern of natural woodland development. Most of the

stands studied had, however, only started to enter into a transitional old-growth stage, and at Denny and Monks Wood regeneration had been blocked or destroyed by severe browsing. It would be particularly useful to map the spatial pattern of stand development at The Mens and Clairinsh where old stands have broken-up and regenerated in patches.

It is expected that at many sites (but not all) a reasonably small-scale and well-structured mosaic will develop over time from these initial even-aged blocks. However, this is highly dependent on their composition and degree to which wind and drought (in particular) disturb the canopy. Where a small-scale mosaic develops and many cohorts are represented in a relatively small area, this will tend to favour shade-tolerant species and marginalize light-demanding types. This was highlighted by the developments at The Mens where beech and holly became increasingly important and ash and birch were largely dependant on the creation of medium-larger gaps. It is also evident at Suserup Skov where the developmental cycle and mosaic pattern have been examined in detail (Emborg 1995, Emborg *et al.* 1996, 2002). It is typical of woods in the southern Appalachians in eastern North America where canopy gaps are mostly small and filled by four species that are able to withstand heavy shading and respond well to small increases in light: the more light-demanding species are limited to a few larger openings (Runkle 1998). Large-scale disturbance is likely to affect only a minority of sites. It will favour light-demanding species like birch and create a very blocky mosaic, as exemplified at Toy's Hill study site.

4.5. Future research priorities in minimum-intervention reserves

Peterken (1993a, 1996, 2000a) has identified that minimum-intervention woodland reserves are necessary as a scientific tool to study and increase our understanding of natural woodland in Britain. These would serve as a reference-point for ecological science, nature conservation management, and the application of nature-based forestry. This requires that: (i) a representative series of reserves is set aside, with priority being given to

original-natural and extant native mixtures and including some wood-pasture sites; and (ii) an appropriate long-term recording system is established and maintained. So far a provisional series of reserves has been identified for England and a list of features to record and monitor therein drawn up (Mountford 2000a). Several reserves have had permanent transects or plots established and re-recorded, as exemplified by the sites included in this study. However, there has been little further development with formalising the proposed series.

The present study shows that such reserves can be used to generate valuable information about the features and processes found in 'natural' woodland in Britain. As the study sites matured they grew away from a managed semi-natural state and developed by natural processes. Moreover, they accrued features that are characteristic of virgin temperate woodland in eastern North America and east central Europe. The oldest stands proved particularly useful as they started to reveal information about disturbances, dynamics and processes in old-growth stands. These are rare and have been scarcely studied in north-west Europe. They are of great interest, as they show much more about the true character of natural woodland and just how this deviates from managed, semi-natural stands.

Nonetheless, all the sites still bore the imprint of part-management and continued to be influenced by various 'unnatural' features. In particular, certain original-natural species were missing (notably lime), other species not found in original-natural woodland were inherited or colonised later (notably Chinese muntjac deer and American grey squirrels), original-natural populations of large herbivores had been altered, and the structure of the stands remained was strongly influenced by the conditions when management activities were abandoned. Even though it is possible to restore some original-natural features and control certain undesirable modern-natural features, it is impractical to completely isolate minimum-intervention reserves from pervasive agents such as grey squirrels. This does

create some real difficulties in using minimum-intervention reserves to understand the dynamics of original-natural woodland, though special attention could be given where this aspect is the main aim of the research. However, it will be less of an issue where the research objectives are aimed at identifying how extant semi-natural mixtures develop naturally. This has a strong practical application, as it should show what natural features and silvicultural treatments could be included in production forests and how minimum-intervention could be used as a cheap and effective management tool in nature reserves.

Particularly useful information was gained from permanent transects, where the actual fate of individual trees and patches of woodland was tracked, and patterns and variations across stands were detected. The transects were straightforward to relocate and record provided they had been securely marked and suitable notes made of their general location. Those that had run for several decades and had been recorded on several occasions were especially useful in demonstrating how long-term stand change differed from one period to another. As a general rule, such transects need to be recorded at least once per decade. In addition, it would be useful to have an annual record of events like tree falls and an immediate recording after major events (notably severe windstorms or drought). Recording in minimum-intervention reserves should, however, not be restricted to permanent transects (see Mountford 2000a, Parviainen *et al.* 2000). There is a strong case for recording features using a systematic series of circular or square plots, as was done at The Mens. This will generate a more representative and statistically valid sample. As was also demonstrated at The Mens, irregular plots and large-scale mapping can be useful to examine details of individual canopy gaps and the landscape pattern of these across reserves. As discussed in Section 4.4.5, it would be useful to map the spatial mosaic pattern of developmental stages across reserves.

The number of features and level of detail recorded in the permanent transects was substantially increased for this study (see Table 2.3). Stems as small as 1-5cm gbh and well-established, low-growing individuals were included, a good deal of time was spent collecting supplementary notes on the condition of stems, and the amount and condition of dead wood, the extent and condition of canopy gaps, and other salient features (e.g. patches of ground vegetation, position of fallen trees and root plates) were also recorded. These proved to be a valuable additional asset as they covered and quantified important aspects that were not included or difficult to pinpoint otherwise. Originally the recording thresholds were set at 1.3m in height for individuals and 5cm gbh or more for stems. However, this failed to include an important part of the regeneration phase and especially potential recruits that are held back or destroyed browsing. Of course, there is a time limit to what can be included and it is not necessary to record every feature in every transect section or for every stem. Subplots can be identified to record small stems, low-growing individuals or even seedlings <30cm tall. Supplementary notes could be kept brief and focus on key aspects, notably cause of death, damage and crown position. Dead wood need not be included. Photographs could be as an alternative or supplement to other records.

The quality and detail of the records inherited varied greatly. Sometimes it was apparent that recorders had not bothered to measure certain features precisely enough. Although this was not a serious issue when it came to identifying broad patterns of stand change, it was problematic when examining specific features, particularly stem growth rates. As basal area increment was found to give the best representation of growth (rather than ring width increment), it is especially important that this is measured accurately. This can be done by measuring stem girth (*not* diameter) to at least the nearest half cm, ensuring that measurements are taken close to 1.3m up a stem on a particular side, and avoiding irregularities and noting where adjustments had to be made for these. On large trees it would be better to mark the position where the trunk is measured.

There are other difficulties associated with such open-ended, non-specific and long-term research, not least sustaining interest, effective archives and funding (Peterken & Backmeroff 1989, Peterken 2000b). This would be helped if long-term research was identified as a fundamental aspect in the site management plan, the involvement of initiators was maintained and passed on, and recording was coordinated and funded at a national level by a well-established institution. In addition, any recording system used must incorporate generalist elements and be somewhat open-ended, repeatable, flexible and reactive if it to be useful. The system used in this study (see Table 2.3) is intended to be generally applicable, though some features will undoubtedly prove more useful than others, and future recorders will probably want to skip certain aspects, include new features, and use a different degree of precision. A major difficulty will be deciding what aspects to include at each recording and the level detail and replication. There will always be a conflict between immediate interests and outputs and aspects that might be useful in the long-term. However, if records are to cover for the majority of eventualities, shortcuts should be strictly avoided and inevitably some will, in retrospect, appear excessive and unnecessary (but this is not a failing). Whatever, experiences have shown that it is useful to keep all records made (including photographs and casual observations), even if they seem rather simplistic and outside of the recording plan.

Taking a broader perspective, it would be useful if a greater range of initial states and browsing regimes were adopted in minimum-intervention reserves used for research. This would help to generate more information from individual sites and provide valuable scientific contrasts. If a range of gaps were created in relatively uniform sites by pulling trees over or killing them standing, then natural regeneration and subsequent transitions could be studied under a wider range of conditions. It might be appropriate to do this at Monks Wood. However, such stands are broadly representative of those that develop after large-scale natural disturbance and the way they break-up under natural conditions is also

of considerable interest. Another useful experimental tool would be to create a range of browsing regimes using different types of exclosure. The latter would be particularly useful at sites like Denny where the contrast between unenclosed and enclosed would be remain great. They could be used widely and seem especially attractive given the widespread increase in deer and the impact they can have on understorey developments. If permanent and temporary exclosures were erected and studied then much could be learnt about the different states that develop when large herbivores are added to the equation. This is of special significance when it comes to our understanding of original-natural woodland: much more use should be made of minimum-intervention reserves maintained under different intensities of browsing to help resolve the significance of the hypothesis that in the original-natural forests large herbivores were abundant and regeneration developed mainly in the protective cover of thorny bushes, as proposed by Vera (2000). They would also help protect at least some parts of sites against sudden unwanted increases in deer, as happened at Monks Wood. Of course, such actions would need to be justified in terms of the overall and site-specific research objectives and other valid issues.

This study has generated a wealth of information on natural stand development and outlined how several native woodland types might develop in the long-term. A major task for the future is to extend this work to include all of the major native woodland types, as recommended by Mountford (2000a) and Peterken (2000a). This does not rule out more artificial mixtures, particularly sites where sycamore, beech, hornbeam and sweet chestnut are allowed to naturalise, and major types of conifer plantation. From a scientific point of view, it would be useful if each type included were in some way replicated. This would be helped if research reserves were coordinated at the north-west European regional level (or even wider). In addition, recording should certainly be maintained (if not extended) at all the sites where it has started. As the stands age they are certain to reveal more about the development and characteristics of old-growth stands, especially the pattern of break-up,

release and regeneration, extent to which shrubs fill gaps, long-term affects of browsing and squirrel debarking, longevity of old, uprooted and damaged trees, and large-scale arrangement of developmental stages. This is a key target area for future research.

4.6. Main conclusions

This study has generated a wealth of information on the features and processes involved with natural stand development in minimum-intervention woodland reserves (MIWRs) in lowland Britain. It has demonstrated that permanent transects/plots are an invaluable tool in this field of research, particularly because they are: (i) simple to maintain; (ii) demonstrate actual changes in individual trees, whole populations and patches of woodland; and (iii) can connect cause with effect, i.e. they are an effective means to show not only how stands and individual elements change, but also why. Nonetheless, this is not the only research approach that can yield important information on natural stand dynamics. In fact, information gained from other approaches is invaluable in interpreting and understanding changes recorded in permanent plots.

Although natural stand development can be observed in MIWRs, such places are not strictly natural (at least in comparison to original-natural woodland). This was exemplified by the six sites studied, which had formerly been intensively used as wood-pasture or coppice. This has altered their structure and composition and, even after many years of little or no direct intervention, remained obvious. In addition, certain species not found in original-natural woodland had naturalised and become significant ecological factors (notably the American grey squirrel and Chinese muntjac deer). If, as has been contested, large herbivores were originally widespread and numerous, then this aspect of regime was also rather natural. Although these aspects limit the value of MIWRs as natural reference sites, it does not entirely invalidate them. The reserves in this study had inherited various natural features and, as time passed, they grew away from a managed state and started to

reflect natural patterns of growth, mortality, regeneration and disturbance at least under modern-day conditions.

The long-term natural development of each of the major native tree and shrub species and major woodland types found in the MIWRs studied depended on a range of factors. Each major species displayed a unique set of characteristics as defined by their: (i) growth form; (ii) ability to regenerate or expand; (iii) shade-tolerance and ability to persist below closed stands; (iv) growth potential on different soil types; (v) maximum height and age; and (vi) vulnerability and response to browsing, wind, drought and other types of damage. The development of each woodland type and individual stand depended on the initial species mixture and structure, the climatic disturbance and browsing/debarking regime, and other factors that prevailed over time. Although it was possible to describe in outline the potential long-term composition of each woodland type, a range of outcomes was identified depending on which species managed to successfully regenerate as and when opportunities arose, the impact of large herbivores and grey squirrels, and the incidence and scale of severe windstorms and drought.

Eight major processes were found to govern the natural development of the stands studied:

(i) *Exclusion* – this was the predominant process in dense, closed, young and middle-aged stands where competition was intense – it had relatively predictable effects, resulting in the suppression of many stems and gradual loss of smaller, less vigorous stems, especially those of light-demanding species;

(ii) *Debarking damage caused by grey squirrels* – this had a major impact on pole-sized beech, especially fast-growing trees released into canopy gaps, though other trees and species were also affected – some trees died after being debarked and others were left with dead crowns and large patches of bark missing;

(iii) *Browsing and debarking damage caused by large herbivores* – this curtailed or prevented regeneration and sometimes destroyed established individuals in the understorey, especially where ponies and/or deer were numerous – damage at lower densities was more selective and certain features provided some protection against herbivore damage;

(iv) *Damage caused by wind* – this mainly affected mature stands – it ranged from the loss of a few branches to major breakage or complete uprooting of trees, and often included indirect damage to individuals in the substratum – some individuals died after being wind-damaged, but others resprouted and made a substantial recovery – wind damage proved to be chronic and relatively small-scale, but in one year a particularly severe storm all but destroyed one of the stands studied – various factors made certain stands and individuals prone to wind damage;

(v) *Damage caused by drought* – this caused dieback and bark necrosis mainly in mature beech and birch and, sometimes, other species – severe drought killed some individuals immediately, but death in other trees took some or many years and involved disorders to which they were normally resistant– only one drought managed to trigger widespread deterioration and led to the partial break-up of one of the stands studied – various factors made certain trees prone to drought damage;

(vi) *Regeneration and release below part-broken canopies* – this took place below mature stands as small breaks started to arise in the canopy – it involved the release of long-suppressed individuals and/or the invasion of a wave of shade-tolerant shrubs and trees, particularly beech, holly and rowan – the effect was most pronounced where the canopy was composed mainly of light crowned trees and more substantial gaps were created;

(vii) *Regeneration and release within/around larger canopy gaps* – this took place where larger gaps were created in mature stands – these became a focus for tree and shrub regeneration, regrowth of damaged individuals, and release of hitherto suppressed individuals – regeneration in smaller gaps tended to be slow growing and mainly of shade-

tolerant species, whereas in large gaps light-demanding trees, shrubs and ground plants recruited and grew rapidly – regeneration tended to be patchy, not least because seed sources/production/dispersal were limiting for certain species, damaged and hitherto suppressed individuals or ground vegetation developed strongly, fallen trees and dead trees shaded the ground, and large herbivores and other mammals damaged potential recruits; (viii) *Release of overstorey trees around canopy gaps* – this took place wherever gaps were created in the overstorey and growing space was made for surviving border trees – small gaps were filled mainly by the extension of existing crown branches, whereas in larger gaps border trees often developed epicormic sprouts on their crown branches or trunk (especially oak) or expanded from low lateral branches (especially beech).

The structure and predominant processes dictating natural stand development were found to change over time. After a stand had regenerated, the basal area tended to gradually increase and peak at about 30-50m^2 ha^{-1} once a stand had become mature. Whilst exclusion remained intense, the density of stems tended to decline, the size-distribution changed from negative exponential to right-skewed normal, and (predominately in stands dominated by light-crowned trees) stratification increased. Once a stand had matured and understorey regeneration/release started, the size-distribution changed and both stem density and stratification increased. Canopy gaps usually remained scarce until stands reached at least 125-150 years growth. Even then gap creation tended to be patchy and with periods of gap closure taking place between episodes of gap creation. The main cause of gaps was wind or drought damage. The volume of dead wood tended to be high immediately after a major disturbance. It then declined to a low level after several or many decades, and increased again only once a stand had matured and large overstorey trees started to die or break-up. Stand development was summarised under four sequential stages (stand initiation, stem exclusion, understorey reinitiation, old-growth/canopy break-up), each being characterised by a set of predominant processes (as implied by their title) and associated structures.

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6. APPENDIX: Common and scientific names of plants in text

Based on Clapham, Tutin &Warburg (1993) and Mitchell (1986)

Common name	Scientific name
Alder	*Alnus glutinosa* (L.) Gaertner
Alder buckthorn	*Frangula alnus* Miller
Ash	*Fraxinus excelsior* L.
Aspen	*Populus tremula* L.
Beech	*Fagus sylvatica* L.
Bent-grass	*Agrostis canina* L., *A. capillaris* L., *A. stolonifera* L.
Birch, downy	*Betula pubescens* Ehrh.
Birch, silver	*Betula pendula* Roth
Bird cherry	*Prunus padus* L.
Blackthorn	*Prunus spinosa* L.
Bluebell	*Hyacinthodies non-scripta* (L.) Chouard ex Rothm.
Bracken	*Pteridium aquilinum* (L.) Kuhn
Bramble	*Rubus fruticosus* L.*sensu lato*
Broom	*Cytisus scoparius* (L.) Link
Buckthorn	*Rhamnus catharticus* L.
Butcher's broom	*Ruscus aculeatus* L.
Cherry, wild	*Prunus avium* (L.) L.
Crab apple	*Malus sylvestris* Miller
Dog's mercury	*Mercurialis perennis* L.
Dogwood	*Cornus sanguinea* L.
Elder	*Sambucus nigra* L.
Elm, English	*Ulmus procera* Salisb.
Elm, smooth-leaved	*Ulmus minor* Miller
Elm, wych	*Ulmus glabra* Hudson
Field maple	*Acer campestre* L.
Foxglove	*Digitalis purpurea* L.
Guelder rose	*Viburnum opulus* L.
Hard fern	*Blechnum spicant* (L.) Roth
Hawthorn, common	*Crataegus monogyna* Jacq.
Hawthorn, midland	*Crataegus laevigata* (Poiret) DC.
Hazel	*Corylus avellana* L.
Holly	*Ilex aquifolium* L.
Honeysuckle	*Lonicera periclymenum* L.
Hornbeam	*Carpinus betulus* L.
Ivy	*Hedera helix* L.
Juniper	*Juniperus communis* L.
Larch	*Larix decidua* Miller
Oak, pedunculate	*Quercus robur* L.
Oak, sessile	*Quercus petraea* (Mattuschka) Lieblein
Privet	*Ligustrum vulgare* L.
Purple moor-grass	*Molinia caerulea* (L.) Moench
Rhododendron	*Rhododendron ponticum* L.
Rose, dog	*Rosa canina* L.
Rose, field	*Rosa arvensis* Hudson
Rose, sweet briar	*Rosa rubiginosa* L.
Rosebay willowherb	*Chamaenerion angustifolium* (L.) Holub
Scot's pine	*Pinus sylvestris* L.

Rowan	*Sorbus aucuparia* L.
Small-leaved lime	*Tilia cordata* Miller
Soft rush	*Juncus effusus* L.
Spindle	*Euonymus europaeus* L.
Sweet chestnut	*Castanea sativa* Miller
Sycamore	*Acer pseudoplatanus* L.
Tufted hair-grass	*Deschampsia caespitosa* (L.) Beauv.
Wayfairing tree	*Viburnum lanata* L.
Western red cedar	*Thuja plicata* D. Don
Wild service	*Sorbus torminalis* (L.) Crantz
Willow, crack	*Salix fragilis* L.
Willow, eared	*Salix aurita* L.
Willow, goat	*Salix caprea* L.
Willow, grey	*Salix cinerea* L.
Willow, white	*Salix alba* L.
Wood sorrel	*Oxalis acetosella* L.
Yew	*Taxus baccata* L.